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of the author of the "Apodidae"
A disciple of Haeckel!



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Some Neglected Factors in Evolution

An Essay in Constructive Biology

By

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Edited by

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With 47 Illustrations

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EDITOR'S PREFACE

THIS book contains the mature results of twenty years of biological research, to which the author brought a mind trained by mathematical and philosophical studies.

In 1889, while working under Professor Haeckel, in the Zoological Institute of Jena, Mr. Bernard took up the problem of the origin of the Crustacea, and from that time onward was continually engaged in research work which covered a wide field.¹

His interest in certain normal and abnormal phenomena of vision known as "entoptic" phenomena, also dating from 1889, led him to make a comparative study of the vertebrate retina, which extended over ten years, and convinced him that the retinal tissue does not consist of "cells," as usually stated, but is essentially a net-work, the nodes of which are formed by nuclei. This discovery led him to doubt the adequacy of the cell doctrine which regards the

¹ Among Mr. Bernard's writings are "The Apodidæ" (*Nature Series*, Macmillan, 1892), "The Comparative Morphology of the Galeodidæ" (*Trans. Linnean Soc.*, 1896), Vols. II-VI of the British Museum Catalogue of the Madreporarian Corals, six articles entitled, "Studies in Retina" (*Quart. Journ. Microsc. Sci.*, Vols. 43-47), and many others, contributed to English and foreign scientific journals, on such subjects as the Sense of Sight, the Origin of the Vertebrata Eye, the Ancestry of the Vertebrata, the Zoological and Systematic Position of the Trilobites and Limulus, and the Morphology of the Madreporarian Corals, the Arthropoda and the Arachnida.

cell as *the* unit of structure of all living tissue, and to consider the cell itself as a tissue needing explanation by some more elementary unit.

A prolonged study of the fine structure of protoplasm generally and, more especially, of those tissues that cannot be satisfactorily explained by the cell doctrine, confirmed the results obtained from the retina, and convinced Mr. Bernard of the universal presence, in living organisms, of the "protomitomic network."¹

While writing the thirteen chapters on this "neglected factor in evolution," which are embodied in Part I of the present work, Mr. Bernard became so impressed with the necessity of recognising more than one unit of structure and also with the traces of a law Periodicity in evolution to which a series of units would give the clue, that he decided to publish a book on this subject before bringing out his work on the protomitomic theory. His treatise on "Periodicity" or "Rhythm" another "neglected factor in evolution," now appears as Part II, in which other factors either wholly or partially neglected are also brought forward, *viz.*, the evolutionary periods inaugurated by the series of units of structure, colony formation as the essential factor in producing new *types* of organic life, and the psychic bonds which, in the human colonies built up by Man, take the place of the physical bonds connecting the units of other colonies.

Since this book is to be regarded, by the express wish of its author, as essentially an "essay in constructive biology," a brief preliminary sketch of its contents may

¹ This term was first used by Mr. Bernard in "Studies in Retina" (*Quart. Journ. Microsc. Sci.*, Vol. 47, pp. 311-327) for the fundamental reticulum discovered by him in the retinal tissue.

help the reader to recognise the general plan of the author.

The subject of Part I is the Protomitomic Network which Mr. Bernard believed to be universally present in living tissues, and to be traceable not only in the most primitive micro-organism but even in so highly specialised a tissue as the retina of the human eye. The essential constituents of this all-pervading network are chromatin bodies and very delicate linin filaments, the fluid or semi-fluid matter associated with these being of secondary importance. The simplest possible combination of these elements of protoplasm seems to yield a hypothetical unit of organic structure (the "chromidial" unit), which is capable of manifesting all the phenomena of life, and is shown to be of great value in analysing the "pre-cellular" organisms for which the usually accepted unit of structure, the Cell, does not satisfactorily account. The simplest known animal forms are shown to be essentially networks, and among these we find the Cell, which the author explains as a colonial organism built up of chromidial units.

The early Metazoa are next described as protomitomic networks differentiated in many distinct ways in response to the demands of different environments. The essential functions of the filaments and the chromatin, already indicated in pre-cellular organisms, are here traced in ever fuller and more varied development. The method of feeding of the early Metazoa receives special attention as one of the chief causes of their differentiation.

In the later chapters of Part I, the rise of tissues and organs as differentiations of the network is traced more in detail. The various forms of epidermis are shown to be modifications of the outermost layer of the

protomitomic network. The sensory organs are deduced from its surface and fringes, a special account being given of the structure of the retina as a witness to the presence of the network. The nervous system also receives a new interpretation. Owing to the fact that every filament of the network is, from the first, capable of conveying nerve stimuli, it is considered as co-extensive with the original, undifferentiated network. After the differentiation of the tissues and organs, the residuum becomes highly specialised as the central nervous system for the co-ordination of the functions and organs of the body, and for the evolution of the psychic functions.

The concluding chapter deals with the phenomena of growth, which are difficult to explain by the cell-colony theory. Even the puzzling process of mitosis can be accounted for by the recognition of the universal presence of the protomitomic network.

Part II deals with the Cosmic Rhythm hinted at by Herbert Spencer, but not hitherto seriously considered as a factor in evolution.

The chromidial unit which, in Part I, was assumed to have built up the network of the protoplast, here appears as the first of a series of five structural units, possessing certain characteristics in common which enabled them to become successful as units.¹ Each successive unit is higher, because more complicated than the last, and each in turn introduces a new and higher evolutionary period. Organic life is thus traced in its rise, step by step, from the level of the Microbe to that of Man.

¹ Some repetition of facts and arguments which occur in Part I was found to be inevitable, since the author intended Parts I and II to appear as separate books.

The production of new *types* of organisms, which is not, as the author shows, accounted for by the Darwinian theory of variation, is considered by him to be due to that special method of colony formation in which the combining organisms, or “units,” fuse together in such a way as to give rise to a new and more complicated organism, a process only explicable when the presence of the protomitomic network is recognised. Man appears as the very complicated unit of the fifth evolutionary period and the social aggregates formed by him are regarded as being serial with the earlier animal colonies. The difficulties encountered when human units, as distinct individuals, have to form colonies, are considered and met by the recognition of psychic bonds as taking the place of the physical connections between the units of the earlier colonies. This leads to a discussion of certain psychic phenomena and theories. Physical and psychical phenomena are analysed and compared with the view of unravelling their relationship in the light of the author’s theories. The “psyche” in Man may be regarded, the author believed, as a “faculty of perception” *i.e.*, as a sensory organ specially developed in this fifth evolutionary period, for the exploration of a psychic environment which has now assumed special prominence. It is suggested, in conclusion, that the cosmic rhythm may, in the future, carry organic life to a still higher level, through the interplay of Man’s developed faculties with an ever widening range of the psychic environment.

Certain factors in evolution, to which due prominence has not hitherto been given, thus help us to obtain a conception of organic life as a whole, which is not only comprehensive but coherent.

Among Mr. Bernard's MSS., several prefaces and prefatory notes were found. A few extracts from these are given to show that he was fully aware of the speculative nature of some of his views and of the opposition they were likely to arouse. But he firmly believed that he had caught sight of new truths of vital importance to the study of the evolution of organic life, and felt impelled to introduce them to the notice of his fellow biologists. His general attitude of mind in facing the great problems of organic life and its evolution and his earnest desire to contribute his share to their solution are also evident in these extracts.

"1¹. The modern specialisation of scientific research has reduced the worker, who, perchance, has made a discovery which seems to him to have a bearing far beyond the range of his own special subject, to a sorry position. He has to stand with his discovery in his hand and try to explain, to a ring of specialists in other branches, how it may or must affect their subjects.

"If he tries to become familiar with all those other branches before he publishes, he will do nothing, for life is short. It is not sufficient to study the elements alone of those hundred and one other subjects, for, if the new discovery is to help, it will, as a rule, do so most at those points where the specialists themselves are in difficulty.

"Consequently, a book such as this, in which evidence is collected from the whole range of the biological sciences, has necessarily to be put out apologetically.

"Within my own special branch of science, the histology of the retina, I can discuss the details of the evidence for my theory with some reasonable confidence, having studied it for nearly twenty years, and the same confidence is

¹ Extracts 1 and 2 are taken from a prefatory note written about 1905 in connection with a book entitled "The Protomitotic Theory," the MS. of which is incorporated in Part I of this book.

justified when reviewing the better known facts of zoological and botanical morphology. But every one who has attempted any original scientific work knows how easy it is to pass from the solid ground of knowledge into the enveloping fog, and to regard its transient shapes as equally solid. The fog clings so close, legitimate inferences are so intertangled with plausible, provisional, probable, and illegitimate inferences, that the greatest acumen, and shall I add, sang-froid, are needed to avoid pitfalls. The prevailing tone of this book should thus be that of interrogation. 'I find this arrangement here, how will it fit into your scheme of things which it must obviously affect?'

"This is, indeed, the attitude I have sought to adopt, but I am conscious that in many cases I have failed, that the humility I feel in my heart may not be very apparent in the text.

"The knowledge that, in my own subject, I stand on the solid ground of ascertained fact may have led me, by chains of argument the links of which it was impossible for me, in all cases, fully to test, to draw conclusions without constantly reiterating that they are to be regarded as provisional and tentative.

"It is hardly to be expected that any of my readers will consider my theory as proven. Every trained biologist may have a score of difficulties to bring forward which are at present not perceived. Time will bring all these face to face with my theory which will have to be tested by them. On the other hand, I feel confident that there are many who, taking a lenient view of the errors in my work, will neither accept nor reject my theory, but will welcome it at any rate as a new instrument for morphological and histological enquiry, and will suspend their judgment until practical observations have shown what its value is in comparison with the theory of the 'cell' which it claims to replace."

2. "I wish especially to emphasise the fact that this is es-

sentially an essay, and makes no pretence at being a learned treatise. It is impossible that, in dealing with so large an array of facts, I have been always correct or up to date in the details; my excuse, if any were needed for such inaccuracies, may be found in the fact that, during the writing of this book, my energies have been largely monopolised by the work on the stony corals with which the trustees of the British Museum entrusted me. It is an essay to present what appears to me to be a possible co-ordination of the facts of biological science as they appear to a single student. To bring the theory into final shape, if it prove worth it, will be the work of future generations of students.”¹

.

3.² “This treatise began simply as an attempt to review the known forms of life with special reference to their organised tissues, for the purpose of showing that they could all be explained histologically as so many modifications of a fundamental network.

“Its principal theme was that the cell doctrine was too crude to account for the phenomena, that what are called ‘cells’ are merely form features of some deeper underlying texture. Consequently, the earlier chapters are devoted principally to the analysis of histological and physiological phenomena which should have a certain value as such, if only in the way of stimulating enquiry.

¹ Mr. Bernard’s hope was that the protomitomic theory might, in time, be fully worked out, and more especially, that young biologists, interested in his researches, might carry them on in various directions, testing his conclusions by their own work.

His researches in connection with the retina are now being continued in this way at the Middlesex Hospital Medical School, by Dr. R. J. Gladstone, Mr. Bernard’s own material having been lent for the purpose.

² Extracts 3 and 4 are taken from a preface written for a book including “The Protomitomic Theory,” and several chapters entitled “A Periodic Law in Evolution,” which are now incorporated in Part II.

“I found it impossible, however, to stop at this, inas-
much as my analysis of living structures on the basis of the
fundamental linin-chromatin network gradually revealed
to me what appeared to be an ascending series of organic
units. I can make no excuse for subordinating my original
theme to an attempt to drag these units from their ob-
scurity and present them to the world for, unless they are
phantoms of my brain, they must have messages for us,
which others may be more fitted to hear and expound
than I am.

“This treatise, however, still remains an Essay in Con-
structive Biology.”

.

4. “This book began as a discussion entirely confined to
an analysis of anatomical facts or what I, with my limited
knowledge of such a vast range of subjects, believed to be
facts. Out of the discussion itself, however, an evolu-
tionary series gradually seemed to rise and to take ever
clearer shape, until it crystallised out into a definite evolu-
tionary doctrine which seems to bring us a stage nearer
the comprehension of the subject.”

.

“The forms of life together constitute a progressive
series, a series which can reveal to us the evolution of the
animal and vegetable kingdoms, a series which we have to
learn to read, for it is the history of life. It contains the
secret of our being, of our past and our future, and al-
though, on its purely physical side, it tells us only of the
physical frame, psychical existence will be found reflected
in it as in a mirror.

“This book is an attempt to deal with this marvellous life
series, in which we individually play our parts.

“We shall study the forms of life and their serial order, so
far as we can make it out, and the nature and causes of the

differences between the consecutive forms of the series. These forms will be passed in review, each in turn being submitted to an analytical process not hitherto recognised. Beginning with the simplest and passing on to the more complex, I shall try to show that my method of analysis reveals relationships not only new but sufficiently startling to justify my having made the attempt. For it is only an attempt and both my method and my conclusions can at best be but crude approximations to the subtler realities."

The MSS. of both the books planned by Mr. Bernard underwent frequent and repeated revision and rearrangement and, at the time of his death, Part II was once more cut up ready for final revision. Consequently, the editor had to select, from a great mass of MSS. written at different times within the last eight years, the matter that seemed best to represent the author's final views, and she alone is responsible for its arrangement in the present work.

In conclusion, the editor wishes to record her gratitude to the friends who have assisted her in her work. Mr. Randolph Kirkpatrick of the Natural History Department of the British Museum read the MS. of the book and repeatedly helped her not only by his expert knowledge but by his unfailing kindness in looking up obscure references in the original MS. and in identifying illustrations which, though drawn under the author's supervision, had remained unmarked and unexplained. Professor Blackman, of the University of Leeds, who kindly read a great part of the MS., contributed valuable criticisms and suggested some of the editor's notes, and Dr. John Cameron of the Middlesex Hospital Medical Schools, an expert on nerves and retina, whose own researches to a great extent confirmed those of Mr. Bernard, was good enough to read

Chapters XI and XII, the most technical in the book, and to draw one of the illustrations.¹

¹ Mr. Bernard, in one of his prefaces, gratefully acknowledges the kindness of Mr. Gerrit Miller of the Washington National Museum who read part of his MS. and discussed it with him. He also expresses his indebtedness to Professor E. B. Wilson's "invaluable treatise," "The Cell in Development and Inheritance" from which he gathered many of the facts he advanced in support of his own views.

M. B.

February, 1911.

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Part I

THE PROTOMITOMIC NETWORK

CHAPTER I

INTRODUCTORY—THE ANALYTICAL FACTORS, OF PRO- TOPLASM MORPHOLOGICAL AND PHYSIOLOGICAL, AND THE EARLIEST RECOGNISABLE UNIT OF STRUCTURE

WHEN making a close comparative study of the vertebrate retina, with the aid of the best histological methods and the highest microscopic powers, I found that the majority of the so-called "cells" of the retina differ very seriously from the orthodox cell.¹ Instead of so many separate masses of protoplasm, each containing a nucleus, I found so many nuclei connected together by exquisitely fine filaments and forming together a continuous network with the nuclei at the nodes. The connecting filaments were seen to be continuations of the filaments within the nuclei, so that the latter appeared to be merely special tangles of the filamentous network.

Again, the protoplasm or cytoplasm which was always thought to be the essential life substance—the nucleus being merely an organ of it—was often entirely absent² or else, when present, its amount and the methods of its association with the nuclei were so

¹ For details and illustrations see "Studies in Retina," *Quart. Journ. Microsc. Sci.*, vols 43-47, and below, Chapter XII.

² This observation has been confirmed by Dr. John Cameron; see *Journ. Anat. and Phys.*, 1905, pp. 144-146.

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variable as to leave the conviction that, however essential it may be to life physiologically, its morphological importance is not primary.

These somewhat startling observations led to years of study of the protoplasmic tissues, and renewed testing of the points at issue, with the result that I came definitely to the conclusion that the nuclei with their filamentous connections represent the essential structural continuity of the tissue under examination, and that the cytoplasm around a certain number of the nuclei represents accessory nutritive or perhaps purely waste substances.

If this new view is true, Sedgwick's description¹ of the cell as a "phantom blinding us to the real structure of organic tissue" is completely justified. For the cytoplasmic masses gathered round the nuclei, which give the appearance of the orthodox cells, not only obscure the extranuclear parts of the network but, in doing so, effectually hide from us the secret of the organic continuity of the tissues, which is revealed for the first time by the discovery of the nuclear connecting filaments. But, as we shall see later, it is the current cell-doctrine alone that is thus guilty of hindering knowledge; the cell exists, and a doctrine of the cell can be constructed which leaves it, if not in its old position as *the* elementary unit of life, at least as one of a series of ascending units.

This observation of the filamentous continuity of the "cells" of the retina had the effect of, as it were, clearing away a mist from the eyes. Semifluid cell-bodies, as the chief structural factors in a tissue more or less homogeneous, gave place to a filamentous network connecting the nuclei together. Filaments, it is true, had

¹ *Quart. Journ. Microsc. Sci.*, vol. 37, p. 87.

often been seen before and also the appearance of networks of filaments. Even the claim that protoplasmic bodies are essentially continuous networks from end to end is not new. But, as we shall see later, it has not hitherto been possible to work out with success any theory of the fine structure of protoplasm as a continuous network.

I might begin this book by a direct attempt to show that what was found in the retina exists in all protoplasmic tissues—that they are all, in essence, continuous networks, and that the nuclei are but special tangles of the filaments of these networks, tangles in which the bulk of the chromatin becomes involved. Further that, in some tissues, namely in those which, with reference to the organs in which they occur, may be spoken of as the metabolic tissues, the filamentous character is effectually obscured by the large amount of cytoplasmic matter required for their activities, while, in other tissues, especially in those which, again in reference to the organs to which they belong, we may call the ergastic tissues, the filaments are the most obvious structural element. Instead, however, of demonstrating this by an extended analysis of tissues, passing from the simplest on to the more complex, I propose to work up the evidence I have accumulated into a connected story or sketch of the organic tissues as living chromatin networks.

I propose to analyse the known forms of living substance into their visible elements, and then, assuming that some of the factors are secondary and non-essential while others are primary and essential, and that constancy is the criterion of the latter, to put on one side the constant factors as those which must have been present

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in the first living organism, or at least in the first organism that became a unit of structure for the building up of higher forms.

This is our first step. The second step is to try to put these constant factors together so as, if possible, to reconstruct a unit which might have served for all known organisms. In this attempt we shall be guided by the fact that these elementary factors are associated with known functions.

This work is necessarily almost entirely morphological. It has to deal with the various arrangements of a filamentous network as so many structures in space. Other considerations will come in, but the sequences are strictly morphological sequences of so many variations of networks or parts of networks, beginning with the simpler and advancing to the more complex. It will be necessary to follow, with the mind's eye, whole series of modifications and rearrangements of the filaments and nodes of the network, and the appeal must therefore be largely to the imagination, yet the imagination of the reader will never long be strained, for our synthesis will, from step to step, be compared with known facts of organic structure and will, I hope, receive confirmation as we advance. But even if this confirmation is not always available, the process can still be rigidly scientific.

The first necessity in this, as in all profitable morphological enquiry, is to be able to distinguish the fundamental structural elements from those which are accidental and physiological. This is not always easy, because the border lines are not sharply marked. Further, all morphological structural elements have physiological significance, although it is not true that all physiological elements have structural significance.

On this distinction depends the value of works on comparative morphology, namely on the proper appreciation of the factors in relation to the essential structure of the organism. Before we can begin a morphological analysis of the forms assumed by protoplasm, in order to be able to arrange them into series which are to have any serious value, it is necessary to discover the essential factors in the building up of protoplasm itself.

Judging from my own microscopic observations and from the records of the observations of others that have come under my notice, living matter seems to yield three or four constant elements.

After eliminating from each kind of the simpler protoplasmic organisms and tissues everything that is accidental and peculiar to it, and retaining only what is everywhere and always present, we obtain some three or four visibly distinct substances. These may, it is true, vary slightly in different organisms in the extent to which they are present and in other non-essential points, but roughly we have:

(1) Chromatin bodies, usually sharply defined, mentioned first because most easily rendered visible by artificial dyeing;

(2) Very delicate filaments, the so-called linin threads;

(3) A highly refractive fluid, the cytologist's nucleoplasm;

(4) A semifluid albuminous matrix in which Nos. 1, 2, 3 always occur and differing from 3 mainly in being less refractive.

These four (or three) seem to be the only essential and therefore the only constant structural factors in all protoplasmic organisms. The chromatin is always

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present either in minute scattered granules or else collected in masses in a nucleus. The linin threads are also always present and, though difficult to demonstrate in some cases, are always to be seen when there is a nucleus, while some fluid matter obviously permeates every protoplasmic mass.

It is in combinations of these three or four substances only that life appears and, whatever the complexities of their combinations, they remain distinguishable to the last. Each has its own form and, as we shall see, its own functions, but these last can be exercised always and only in the presence of the other factors. Whether they pass chemically into each other and to what extent this may be the case, I do not know; in their forms they remain constant and distinct.

The chromatin appears typically in microscopic particles which have been variously named chromidia, chromoplasts, chromoplastids, and so on. These may collect into what look like solid aggregates usually called chromosomes.

These chromidia and their aggregates, the chromosomes, are always found in intimate association with the linin fibrils which stand second in our list of fundamental substances. From the appearance, they might be threaded upon the filaments, although that must not be thought to represent the real relationship between the two, which is probably of the most intimate chemical nature.

The fibrils are of such tenuity that only under favourable circumstances can they be seen under the highest powers of the microscope. When, however, chromidia or other substances taking stain are scattered about on them, then their courses can be traced.¹ Although

¹ See pp. 45 and 248.

the presence here and there of these fibrils and even in some cases their association with the chromatin has long been established, their full extent and importance has not hitherto been perceived and the chief purpose of the first part of this book is to demonstrate the fact that they, with their associated chromidia, form a continuous network as an organic system underlying and commensurate with every organism.

The two other fluid materials, the nucleoplasm and the albuminous matrix (if they are really two and not one, seen under two different conditions), do not here require special attention, inasmuch as their morphological importance, though by no means negligible, is yet secondary. They will find their places in the sequel sufficiently often for all purposes. We may here, however, briefly state that the nucleoplasm is a highly refractive fluid, apparently in intimate chemical association with the chromatin, and therefore specially visible in the nuclei. The albuminous matrix is a fluid or semi-fluid material, which occupies the meshes of the extranuclear network and in which, consequently, the linin threads and the extranuclear chromatin are constantly bathed.

Each factor, besides having its own form, also has its own function, but, as already stated, only in the presence of the other factors. It will, however, be simpler if we attempt a preliminary synthesis before we describe the functions of the separate factors.

It is obvious that the simplest combination of these factors is a network of the linin threads with the chromatin particles at its nodes or otherwise distributed along the threads, the whole being embedded in and commensurate with an albuminous fluid matrix.

We are guided to this, practically, by the known facts

of structure presently to be related, and theoretically, by finding in the retina a network of linin filaments with linin-chromatin tangles at the nodes. We may argue legitimately that, since linin filaments supply the principle of continuity to a tissue, a network is the only conceivable method by which the threads can form a continuous whole. The simplest satisfactory combination of the given factors is, in fact, a linin network with chromidia at the nodes, and such a network might well supply the essential framework of the raw material of life, out of which all its myriad forms have been moulded. But it is obvious that a network of this sort somewhat eludes us as an instrument for morphological analysis. A network without clear limits is, to all appearance, too indefinite to be the chief factor in a science of form. This difficulty is, however, overcome the moment we take into consideration the elementary functions attributable to the parts thus combined. We then find that the network splits up into physiological units and these guide us to the definite form we require as the starting point of our subsequent morphological enquiry.

A network such as we have sketched can very obviously be divided up into many separate nodes, *i. e.*, separate chromidia, each with a certain number of radiating filaments, and each such minute radiating body may be thought of as being embedded in a droplet of the fluid. This appears to be the smallest conceivable organism that contains all the essential elements, each preserving its distinctive form: the chromatin as a minute round body, the filaments projecting from the central chromatin, and the fluid matrix, either homogeneous or differentiated into an inner and an outer layer.

Not only are all the essential elements present in the hypothetical body thus constructed, but it must be capable of manifesting all the phenomena of life. In this first description it must be admitted that we are drawing largely upon what are either well-known facts or facts that will be established later on in this work. But, just as I have somewhat arbitrarily selected for the reader what I consider to be the only constant structural elements in protoplasm without being able to take him through any of the thousands of preparations the study of which led to the selection, so now again, also arbitrarily, I have to state the conclusion I have arrived at as to what are the simplest, most elementary life-functions of these same elements, and, consequently, of the simplest organism they build up.

Taking first the functions of the filaments, we find:

(1) They are contractile, *i.e.*, they can shorten and lengthen again with rapidity.

(2) They can lengthen permanently, *i.e.*, grow.

(3) They can shorten permanently.

(4) They can split longitudinally.

(5) They are the paths along which nerve stimuli run from the periphery to the centre and back.

(6) They are the paths along which most of the compounds resulting from the interaction of the chromidium or central chromatin mass with the matters absorbed from without travel to or towards the periphery, to be got rid of at the surface as waste or to be utilised in the interests of the organism; in the latter case, they are the distributing and arranging elements. The functions exercised by the filaments in such cases may be comprised under the term "synthetic."

(7) Chromatin in different forms, *e.g.*, as chromidia or aggregates of chromidia, also appears to travel along

these same filaments and from them it seems, indeed, never to escape until it passes off in combination with other substances as a secretion or excretion.

These appear to be the simple, elementary functions inherent in the filaments, not apart from other constituents, but in the presence of the other essential structural factors of protoplasm. Some of these functions will be readily admitted by biologists, evidence for the others will be found as we carry forward our application of this method of analysis into the better-known regions of anatomy and histology.

The functions of the chromatin are mostly chemical, and therefore not easy to describe, except in terms of chemical processes. One visible function, however, can be noted for certain, and that is that the chromatin is able to increase in amount up to some small limit, on reaching which it divides into two, and we add to this the fact that it travels along the linin threads, though it cannot leave them until, in combining with other substances, it passes away as an excretion at the surfaces, or builds up some substances in the meshes of the fundamental network.

The most obvious functions of the fluid element or elements, apart from their chemical interactions with the others, seem to be to supply a supporting matrix for the delicate complex of linin threads and chromidia, and apparently, also, by their powers of absorption, to keep the organism fully expanded as it grows. The part played in growth by what is called turgescence has long been recognised, but hitherto without real insight into its significance.

This definite and precise association of the different functions with definite structural factors is admittedly somewhat daring, but again I must appeal

to the evidence brought forward later for every single assertion here made.

Our preliminary process of destructive analysis has thus revealed a very instructive biological unit. We have analysed out both the structural and the physiological phenomena of organic life (passing, but not forgetting, the more intangible psychical phenomena); and when we put together in the simplest conceivable manner what we find to be constant and universal, we arrive at something that proclaims itself an ideal biological unit,—ideal because it is at the same time both a morphological and a physiological unit. It is also obviously a structural unit, for it is one of the nodes of a reticular linin chromatin system which, as we shall show in detail in the sequel, is the essential structural factor in all organic life.

CHAPTER II

PRE-CELLULAR EVOLUTION—FROM CHROMIDIAL UNIT TO CELL UNIT

HAVING found, in the last chapter, a possible structural unit as a starting point in the evolution of organic life, we can begin our attempt to sketch the evolution of the next higher unit, the "cell." Before doing this, however, let me remind the reader that this earlier pre-cellular section of the evolutionary story must necessarily be to a great extent merely suggestive of the way in which the protomitomic theory of the structure of protoplasm¹ might be applied to such a problem. The evidence we have in favour of certain hypothetical early stages in the development of the protomitomic network is, I admit, slender and very incomplete. There are, indeed, not enough facts of the fine structure known with which to compare our hypothetical reconstructions, the special prominence of the filamentous elements demanded by our whole scheme having so far eluded the majority of microscopists. The real foundation of the theory will be found in the chapters that deal with the period with which biologists and histologists are most familiar, that from the cell upwards. If the arguments there brought forward can be established, that will go far to confirm this earlier and more hypothetical portion of the story.

The chromidial unit, hypothetically reconstructed

¹ See Preface, p. x, note 1.

in the last chapter, was described as consisting of a single central chromidium from which a certain number of (probably short) linin filaments radiate. This stellate linin chromatin mass must be thought of as embedded in a minute drop of some fluid albuminous matrix to the surface of which the filaments extend. Its life, like all life on the purely physical side, consists of the sum of its reactions to its surroundings. The whole complex has the power of absorbing various materials from the surrounding medium and of making fresh compounds out of them, and the forces released in these chemical processes supply the energies necessary for its "vital" activities. Without attempting here to dip into the nature of these complex reactions, we may briefly say that, for the development of the organ itself, the most important results are the following:

(1) The chromidium, which appears to be the chief centre of all this chemical activity, is able to add material to itself and to grow.

(2) Material is added to the filaments, which lengthen.

(3) Material seems (perhaps only as a later development) to be stored in positions of unstable equilibrium, so that the energies of the reactions come into play only on this equilibrium being disturbed. This storage of potential energy plays a very great part in all subsequent evolutionary stages and its beginnings may be legitimately attributed to the earliest and most quiescent stages.

(4) The waste matter resulting from these chemical reactions, whether simple and direct or exploded by nerve stimuli, is, in part at least, conveyed away from the chromidial centre by means of the radiating filaments. In the simplest stages, this waste was probably

brought to the surface of the drop and deposited on that surface as so many rings of matter spreading out round the tips until the rings or discs met, and eventually formed a protective pellicle to the organism. This last detail may at first sight appear purely fanciful, but it will be found later that, in this as in all the descriptions above given, we are only ascribing to the unit the simplest beginnings of phenomena well known in the higher forms. The universality and importance of this synthetic function of the filaments throughout all life will be abundantly proved.

(5) As this unit grows by the addition of materials to its chromidium and by the lengthening of its filaments, it naturally also increases in size, and more fluid matters are absorbed from the medium; the chemical reactions take place on a larger scale, more waste products are produced and are carried out by the lengthening filaments to be either ejected or, as above described, spread out on the enlarging surface, thus extending or thickening the protective pellicle.

(6) Lastly we have to mention the special elementary functions of the filaments, only possible apparently in the presence of and in chemical association with the chromatin and the fluid matrix. Reaching the surface, their tips fill the centres of the discs which form the protective pellicle. These tips are sensitive. Impacts of various kinds, mechanical or chemical, act upon their molecular structure and the impulse travels inward as a nerve current which causes molecular disturbances of various kinds. The filament itself may contract, chemical reactions between the stored materials may be started, and other complex phenomena may run their appropriate courses.

We have thus made a first start with our primitive

unit of structure endowed with the simplest known functions. We have seen that it grows, and now we have to follow the results of that growth.

Growth in organic life never means increase in bulk by simple addition, but increase by a process of division and consequent multiplication of units. In the case of our unit, the chromidium seems to reach a size and the filaments a length at which the stellate arrangement is probably no longer able to function and it is found that the chromidium divides into two, the star beginning in this way to change into a network. This could take place by the division of the chromidium first into two, then into four, eight, and so on, with longitudinal splitting of certain of the linen threads and the growth of others in length, as further explained in Chapter XIII and illustrated by Fig. 39. The threads that have to split are those lying in or near the plane of cleavage of the chromidium and the threads that lengthen are those at right angles to that plane. This process, with the moving apart of the chromidia, would produce an organism built up of stars which, by the union of their rays, together form a continuous chromidial network with the chromidia at the nodes.

Hypothetically, the growth and extension of such a simple and uniform chromidial network might continue indefinitely until very large organisms of the same simplicity of structure were produced. But, as a matter of fact, increase in size would sooner or later necessitate differentiations resulting in very important modifications of the whole structure.

Before going on to suggest what these further differentiations would be, let us stop for a moment to see whether there are any facts or current theories which find a parallel in the stages so far described. We do so

in order to let the perhaps bewildered reader feel that he is at last beginning to touch ground.

In the first place, let me call attention to some of the figures given in text-books and intended to illustrate Bütschli's theory of protoplasmic structure.

These figures, which are very widely accepted, show essentially the structure deduced hypothetically from

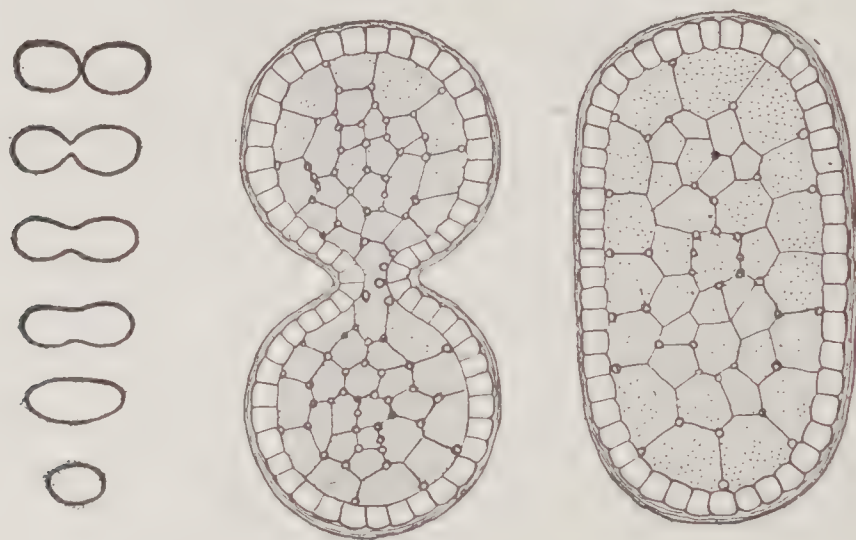


FIG. 1

The fine structure of a Micro-organism (*Achromatium*)
according to Schewiakoff.¹

our unit, viz., small organisms surrounded by a pellicle and traversed by a chromidial network. At the side are shown the visible stages in the division of the chromidia. But an organism such as this is considerably in advance of our hypothetical unit, inasmuch as the chromidial network is already rather extensive.

May we not legitimately ask whether any still smaller organisms than these exist,—organisms small enough to correspond with our hypothetical unit? Surely the answer is and must be that the existence of

¹ *Morph. Jahrb.*, Bd. 13, 1888, pp. 193-258, Pl. 2.

such organisms is very probable. Not only are the innumerable micrococci, for instance, very much smaller than any of the organisms figured by Bütschli and others, but many of these micro-organisms are known to break up into spores of excessive minuteness. If these have any representative of the chromidial network within them it could hardly be larger or more complicated than what has been described as our unit, viz., a single chromidium with a stellate arrangement of linin threads.

These facts, so far as they go, fall in very well with our new evolutionary sketch, but they are admittedly very scanty and I am not relying upon them as demonstration. We shall find the support we want only when we come to the analysis of the post-cellular stages. But if the facts are few, theories abound. Two of these have special interest for us, upheld as they have been by biologists of repute who have supported them simply because they seem to express the truth as nearly as it can be seen.

The first of these is the famous "foam-structure" theory of Bütschli. We shall have to discuss this more fully later on but I would here remark that every section of an organ with such a structure shows a network, and that network is all that can, for certain, be made out. Now I would ask the simple question whether, after all, that network does not represent the true structure, whether the "foam-structure" is needed at all? Later on I shall show that it is not, and in the meantime I shall claim that Bütschli's beautiful figures of sections are so much evidence for a continuous underlying network, *i.e.*, for one of the chief elements of our theory. The other element, viz., that masses of chromidia form the nodes, finds support in the granular theory associated

with the name of Altmann. Basing his views upon the numbers of granules of different kinds present in protoplasmic bodies, and observing that these granules seemed to display all the ordinary vital phenomena of growth and multiplication by division, this biologist was led to suggest that protoplasm, as we see it, is, in essence, an aggregate or colony of elementary organisms of a much lower grade than the cell. These elementary bodies could, in all probability, be regarded as the ultimate, highly complicated molecular groups in which life resides, persistent, free, and variously specialised representatives of which may be seen in the smaller microbes.

Bütschli's theory consequently seems to support the existence of our network, and Altmann's, with its dividing living granules or "biophors," that of the chromidial nodes of that network. The above sketch of the structure of protoplasm out of a linin chromatin network thus reconciles and unites two well-known and widely accepted theories and should therefore be welcomed by biologists.

In Altmann's granular theory, moreover, we find traces of a pre-cellular unit, viz., the biophor; he has, as it were, anticipated the conclusion at which I have arrived as to the chromidial unit out of which the cell unit is built. But beyond the bare suggestion of the possibility of a pre-cellular unit the biophor theory could not take us, for it knew nothing of the essential filaments. How necessary these are for any understanding of the evolutionary process is illustrated by the fact that one of the chief obstacles in the way of the granular theory has been the difficulty of imagining how these separate and distinct granules or biophors could unite into a co-ordinated whole, as they must

have done to form a cell, which is so obviously both a morphological and physiological unit. Indeed, as we shall see later on, we have, in essence, the same difficulty to encounter as in the cell colony theory of the metaplasts, where the great crux is the difficulty of accounting for the co-ordination of separate and distinct cells into a continuous whole. The protomitomic theory of the fine structure of protoplasm overcomes this difficulty, in both cases in the same way, viz., by calling attention to the overlooked connecting filaments. No colony formation of distinct and separate individuals takes place, for the individuals are all along held together into a connected whole by filaments which are at the same time most important structural elements. The division is a division of chromidia—or of nuclei—without rupture of the all-important filaments.

Supported thus, (1) by a few actual observations as to the fine structure of certain micro-organisms and (2) by noting that our view not only harmonises with two well-known and hitherto irreconcilable theories but removes from one of them the chief difficulty in the way of its acceptance, we may continue our synthetic evolutionary sketch with more confidence.

We have reached the stage in which the primitive organism consists of a simple uniform network with chromidia evenly distributed at the nodes, the whole embedded in an albuminous matrix and probably surrounded by a delicate pellicle. Our business now is to try to sketch the lines of the differentiation such an organism would probably undergo as it grew beyond a certain small size.

In the first place, it is clear that only in the case of very small organisms could the environment be con-

sidered as uniform. Mere growth in size would sooner or later cause the relationships of any organism with the surrounding medium to show more and more marked variations at different points of the surface as the strains put upon it gradually increased in force and in variability.

Organisms that settled on the ground would necessarily have a protected, resting part in contact with the substratum and a part exposed to numerous and varying impacts and needing support. Other organisms, again, would float or else would propel themselves through the water, and would develop all the differentiations inseparable from locomotion. There would be front and back, upper and lower contacts with the medium through which the organism passes.

We cannot enter into these cases in detail here. We have not enough data to make such discussion profitable. We can only dwell upon one or two points illustrative of the nature and character of the organism whose later variations it is our business to trace and, fortunately, to trace into regions better known than those in which we are now groping our way.

It may, I think, be laid down as a general principle that the safety of the organism would, in the majority of cases, lie in the concentration of its powers of reaction and response,—concentration at those parts of the surface where the environmental stimuli were strongest and most numerous. In an organism with the constitution we have been describing, such concentration would clearly mean a closer clustering of the chromidia at the needed points, with re-arrangement of the filaments into strands for more direct conduct of stimuli and for stronger and more co-ordinated contractions.

In cases where the organism we are dealing with had to propel itself through water, the means of propulsion were close at hand in the tips of the fringe of the network. We have to think of each of these tips as reaching the surface in the centre of a disc of pellicular matter which it had brought there, the whole pellicle having been formed by such discs meeting and joining. In such an arrangement, the tips of the filaments come into direct contact with the medium, into which they might project beyond the pellicle. In this way we can conceive of cilia being produced. As we shall see later, some special concentration of chromatin is needful for the energy of these cilia, a fact which enables us to postulate special supplies of chromatin in positions where the organism has any particular strains put on its energies.

This principle of concentration of chromidia and rearrangement of filaments for the purpose of stronger and quicker reactions involves three others which cannot be overlooked, for they play important parts in the economics of living organisms.

The first is that any such changes as we have suggested as starting near the surface would gradually spread inward across the whole network, inasmuch as it is impossible to imagine new strains being put upon any part of a *network* without being sooner or later distributed in various degrees over the whole. Concrete cases illustrating this principle of progressive centripetal differentiation will be given later. But for our immediate purpose it is necessary merely to point out that all the stimuli will meet in the centre, where they will either neutralise or strengthen one another, thereby lessening or increasing the intensity of the response of the organism.

A second principle is that if, in reaction to special stimuli, concentration leads to the formation of local clusters of chromidia from which the filaments radiate in closer strands, specialisation may take place in these clusters; in some one function, in others other functions may be prominent, called forth by the special nature of the most frequent impacts of the environment in their immediate vicinity.

The third and last principle to be mentioned is entirely different and contrasts with those described above which are all active and responsive; this last is passive and, as it were, shrinking. It, however, plays an enormous part in life at every evolutionary stage, from the lowest, such as we are now contemplating, to the highest. It comes into play almost everywhere where nutriment necessary for growth and reproduction is obtained without exertion. Organisms under such conditions may remain passive, merely thickening their protective pellicles, and, in this condition, are sufficiently secure from dangerous impacts to be able to survive and multiply. To such passive reaction may be attributed the persistence of countless millions of microbes. The toughness of their coverings and their resistance to all ordinary adverse conditions is well known. They can live and grow in nutrient fluids and multiply with a rapidity which reveals a perfectly startling energy of growth and sub-division in these simpler forms of life.

While these root principles, which seem to govern the reaction of organisms to their environment, account for many differentiations and specialisations of the simple uniform linin chromatin to which our synthetic process has brought us, we are, for the moment, only interested in one which results in an organism that is not modified for any special environment, and thus

remains, as it were, free and ready to react efficiently to any environment at any time. Theoretically, such an organism should be spherical in shape and free-living, and should have a uniform surface, and all its scattered chromidia should be collected in the centre. The centres of energy would then be at the spot where all the paths of all the nerve stimuli from the surface have to cross each other and, conversely, we should have the source of all the energy of response equidistant from all parts of the surface. We should thus obtain an ideal organism, fit for almost all emergencies and able to respond to any call. This would not be the case with organisms which had settled down to some special environment to which they had become adapted and in which alone, consequently, they could live.

The migration of the chromidia to the centre in the hypothetical organism we are sketching naturally involves re-arrangements in the way of lengthening, shortening, and re-grouping of the associated filaments, which would transform the condition of a simple network with the chromidia evenly distributed at the nodes into one of great complexity, yet by no means difficult to describe in its general features.

The chromatin, *i.e.*, the great bulk of the chromidia, will be gathered into the centre into irregular masses due to the re-clustering of any earlier secondary clusters that may have formed, and all these masses will be connected together by a complicated network. Immediately round this central tangle vast numbers of the tangentially arranged connecting filaments between the clusters will be felted, having also had to travel inwards with the clusters they connected. Round this central mass of chromatin and tangled filaments

the great bulk of the network will be arranged radially in anastomosing strands which run to the surface.

If we add to this the nucleoplasm or fluid which seems always associated with the chromatin, we shall have the clusters in the centre bathed in this fluid which, if it had a high surface tension, would force the tangle of the more concentrically arranged filaments round the centre into a close feltwork. The chromatin would thus be seen, either suspended on filaments within a fluid vesicle or massed on the inner walls of the membrane like a felt.

In the interest of more efficient because more perfectly centralised and co-ordinated activities ready to respond to the impacts of the environment felt at any point of the surface, the simple, primitive chromidial network thus becomes transformed into a new organism, an organism which is none other than the Cell. The chromatin, or the great mass of it, is centralised and stored in a specialised portion of the reticulum, the Nucleus, and from that store it passes out when wanted and to the point where it is wanted. The extra-nuclear portion of this contractile and nervous network is equally specialised, being no longer evenly and symmetrically distributed as a network with uniform meshes, but condensed into branching strands, which radiate outwards so as to form the shortest and quickest channels along which the stored up materials in the nucleus can travel to and from the periphery. By such an arrangement, these materials come into more rapid and effective contact with the environment than was possible when they were evenly distributed over a uniform network.

I admit that it may appear somewhat hasty to assume that the result of the processes of gradual centrifugal

differentiation which have been sketched is a typical cell, though the superficial resemblance is striking. Such an assumption plunges us into the very midst of some of the most important controversies as to the finer details of cell organisation. I shall endeavor to prove in detail, however, in the next chapter, that the ideal organism which we have reconstructed enables us to co-ordinate great numbers of scattered and, at the present time, often contradictory observations as to the real structure, character, and functions of the cell.

With our chromidial units we have thus built up an organism which is of the highest possible efficiency for a special level of organic complexity and which is equally adaptable to all possible positions and relationships, an organism, in fact, which possesses all the qualities to make it a new structure such as we know the cell to be. If we can only show that our description of this organism agrees with what is known of the cell, we shall be able to understand how the cell has become the successful structural unit biologists almost unanimously consider it to be. It is obvious that no specialised form could make an ideal unit; only a form endowed at all points with the best powers and one most highly developed on the special level of complexity arrived at could possibly fulfil such a part. Such an organism has here been reconstructed.

The last point I would here emphasise is that such a cell-unit would be a kind of repetition of the chromidial unit. Both have their sources of energy concentrated in their centres, and from these the linin threads radiate to the periphery. The cell, however, differs from the chromidial unit (1) in the greater complexity of the arrangement of the two essential elements, (2) in the greater amount of its chromatin and thus of its potential

energy, and (3) in the far greater strength of contraction possessed in the multitude of linin filaments, and possibly in their increased sensitiveness to variations of nerve stimuli. The cell is thus capable of much stronger responses to a far greater range of possible stimuli. In a word, its "life" is larger.

CHAPTER III

PRE-CELLULAR EVOLUTION—THE PART PLAYED BY THE FILAMENTS

SINCE the evidence to be brought forward in this chapter in support of the pre-cellular evolutionary stages described in Chapter II is, for the most part, indirect, it is somewhat difficult to decide in what order to introduce it. I might, for instance, begin by asking whether any organisms other than the Microbes that were cited as the probable living representatives of the earliest growth stages can be brought forward to illustrate any of the higher stages in the series; or, again, whether any of the chromidial clusters appealed to as explanatory of the origin of that most characteristic organ of the cell—the nucleus—still persist as witnesses of the fact that such clustering ever took place; or I might discuss in detail the question, Does the ideal cell-unit yielded by our sketch really correspond with the orthodox “cell”? Absolutely satisfactory answers to any of these enquiries would go far to confirm our theory. I shall, however, have to be content with giving partial answers to the first and second questions, and a fuller and, to my mind, most satisfactory answer to the third enquiry, the one as to whether our construction of an ideal cell-unit corresponds with the cell known to biologists.

With regard to the existence of organisms which may represent any of the hypothetical stages of our sketch, when we leave out of account the Microbes which, we claim, illustrate the early simple chromidial network and look for some organism showing the early clusterings of the chromidia, we find ourselves on ground which, indeed, requires further working out. The evidence we have is not quite satisfactory, but it certainly points our way. Organisms are now known to exist which possess a very simple network structure with chromatin granules scattered fairly uniformly over the whole. Others there are with uneven clustering, and others, again, with clusterings showing distinct concentration round definite bodies. These are generally regarded as having "distributed nuclei," a term which leaves it open whether such scattered nuclei are a progressive stage leading on to the concentrated nucleus of the cell, or degenerative stages representing the disintegration of the typical central nucleus. From my point of view, the former is certainly the case,¹ but for those who regard the orthodox cell as the first unit of structure, the latter view alone is possible. This latter view, however, is purely dogmatic and quite unilluminating in view of the difficulties of the cell-doctrine, while our view is the very reverse; for we shall find tissues that cannot be explained by the cell, but that are explicable by the chromidial unit, the cell itself, indeed, being one of these. With regard to the various distribution of

¹ The belief that, in these distributed nuclei, we are dealing with progressive aggregations and not with degenerative processes will be confirmed when, later on, we come to trace the chromatin in its movements, and when we find that there are reasons for believing that all the larger granules and masses of chromatin are, in reality, aggregates of chromidia, into which they can, at times, be seen to break up.

chromatin granules, the very fact that they are found quite scattered or in various kinds of clusterings, and even sometimes clustered and sometimes scattered in one and the same organism, suggests that they represent so many attempts to evolve the perfected nucleus of the cell.¹ Of special importance to us is the fact that it seems possible to arrange them into a definite progressive series as so many different kinds of clusterings of separate chromatin granules, some very minute, either single chromidia or small clusters of chromidia, others, larger, yet still somewhat scattered, and others, again, still larger, with traces of concentration and even of the formation of an enclosing membrane.

Thus, although I cannot point to any organisms still existing which might be claimed as exactly corresponding with any of our hypothetical stages, it seems to me that we have evidence of even a stronger character, since there are several cases of organisms which show a series of almost equivalent stages, special interest attaching to the forms in which the granules are found, at one time collected together, and at another scattered over the network.

This field, I admit, requires a great deal more investigation, but, when all the evidence is taken together, it seems highly probable that the early forms with "distributed nucleus" represent some of the divergent forms which would be certain to branch off from the direct line and become fixed in adaptation to circumscribed environments. When discussing the cellular period of evolution, we shall find such vast multitudes of what we may call divergent organisms that, if we grant pre-cellular evolution at all, such forms might be

¹ See Calkins, *Ann. N. Y. Acad. Sci.*, xi, 1898, p. 379.

expected to appear in a pre-cellular period as well; less numerous, it is true, because of the greater simplicity of the organisms of that period, but far more numerous than we as yet know. Later on we shall have occasion to call attention to certain forms still of vast importance in the economy of life which are possibly survivals of this pre-cellular period.

Passing on from organisms with so-called "scattered" or "distributed" nuclei to the organism with the finished nucleus, we have, first of all, as briefly as possible, to sum up the recorded observations on cell structure and to show in what way they support our main thesis. It may not be possible to prove that the evolution of the cell actually ran the course we have described; but strong evidence will be afforded that the cell has a structure consonant with that origin. It is obvious that if our synthetic process, applied on definite and yet simple and intelligible principles, has yielded us an organism which is found not only to correspond with the cell, but even to explain certain hitherto obscure structural details of its organisation, we shall have a strong argument in favor of the validity both of our method and of its results. And this argument will be further strengthened if we can show that physiological processes involved in the sketch, such, for example, as the movement of the chromatin from place to place within the organism along the filaments of the network, are universal phenomena.

According to the protomitomic theory, the cell is primarily a continuous linin-chromatin network with a differentiated centre which is a storehouse for chromatin, the whole being embedded in an albuminous semifluid matrix. According to the cell doctrine, the cell is

primarily a mass of protoplasm with a central organ, the nucleus. From this latter point of view, the cell can be conveniently—and not merely topographically—divided into “cell-body” and nucleus. The accepted view of these two parts of the orthodox cell must now be briefly given and then discussed from the point of view of our evolutionary scheme, and an attempt made to show how our hypothetical sketch illuminates the whole subject.

With regard to the “cell-body,” also called the cytoplasm, we find a steadily increasing tendency to believe that it is fundamentally fibrillar in structure, because of the many and various apparitions of fibrils or networks seen running through it, none, however, having sufficient constancy to make the case certain. Hence, the fibrillar structure of the cell-body is not yet considered to be definitely proved. A rival theory, based upon the fact that protoplasm frequently has a foam-like appearance, has already been mentioned. No final decision has yet been reached as to which of these theories of fundamental structure is correct.

The fact that some cells show a distinct fibrillation is, in itself, no more an argument for the fibrillar structure of protoplasm than is the fact that some cells appear to consist of a foam-like mass of fluid globules an argument in favor of its alveolar structure. Against both of these may be pitted the many cases in which protoplasm appears as a perfectly homogeneous semi-fluid mass. These different appearances have been recorded times without number. In view of the fact that the fibrils seem, in many cases, to come and go, and that the alveoles can sometimes actually be seen forming, the safest *prima facie* conclusion arrived at by Professor Wilson is that “down to the present limits

of microscopical vision," protoplasm is homogeneous, both the fibrillar and the alveolar structures being secondary.¹

Such a conclusion cannot, however, satisfy the upholders of either theory. The "Mitomlehre" of Flemming rests confidently upon the facts that, in many cells, the fibrils are permanent, that, in all cells, they appear at certain times and that, when they are permanent, they are found intimately associated with important vital functions common to all cells. These facts point unmistakably to the existence of the subtle fibrillar substance which, for some reason or other, comes occasionally into view, but which is normally beyond the powers of the present microscope. The protomitomic theory confirms every word of this and explains these occasional appearances as follows: the exquisitely delicate linin fibrils which constitute the lines of functional activity are, at times, coated with chromatin or chromatin combinations and are thus rendered temporarily visible. At all other times, they are quite obscured by the granular cytoplasmic matters which mass round the nuclei.

Again, Professor Wilson's summing up (just quoted) will not satisfy the adherents of the alveolar theory. Not only, it is maintained, can the alveoli be seen in scores of cases, not only can such a fundamental "Wabenstruktur" be linked on with such physical compounds as emulsions, not only can it be used as a powerful instrument in morphological analysis,² but all the assumed fibrillar structures can be shown to be easily deducible from it by assuming the fenestration

¹ *The Cell, in Development and Inheritance*, p. 46.

² Cf. Bütschli's *Protoplasm* with its analysis of the fine textures of tissues in the light of his theory.

of the walls or surfaces of contact and the straightening out and specialisation of the lines that mark the borders of these surfaces.

Now, it is clear that the upholders of the protomimetic theory may leave these rival theorists to fight out the matter between them. Either theory can be made, so far as it goes, to support our main point. For this part of our argument, it does not seriously matter whether the fibrils were fibrils from the first, as sketched in our hypothetical unit, or arose secondarily from a primitive foam structure, so long as we have the fibrils as the chief textural factor of the more complex protoplasmic structures. But there are weighty considerations which compel me to believe that the fibrils were fibrils from the first and that it is not only unnecessary but somewhat disconcerting to have to assume a primitive foam stage. Such a stage is chiefly wanted in order to link on protoplasm with emulsions because of the possibility of thereby explaining certain vital phenomena. It is not necessary in order to explain the foam structure frequently seen in living protoplasm, because that can be easily accounted for by assuming fluid globules to be caught in the meshes of a fibrillar network. And it is a little disconcerting, because the network is not the only factor of importance; the network is invariably associated with chromatin, and the granules of chromatin are seen to be specially associated with the fibrils, and this association, being invariable, may be assumed to be primitive. In order to come to this secondarily through a primitive emulsion stage, it is clear that the primitive emulsion must fundamentally change its whole physical constitution. For the spheres of fatty matter must entirely lose their significance, while the intervening spaces between

the fat globules filled with diffused alkaline fluid would have to become the principal structural elements and assume contractile and nervous functions! These difficulties doubtless are not insuperable but, we ask again, are they necessary?

No such transformation is required by the protomitotic theory. We start from a single chromidium with radiating linin filaments which are contractile and nervous and together form a system within a semifluid globule of albuminous matter. This, as we have seen, appears to be the simplest unit that we can put together out of the structural elements at our disposal.

Be this as it may, I repeat that, as a mere argument, both these theories can be brought in as evidence for the protomitotic theory, since both point to a texture of the "cell-body" which is either primitively or secondarily a reticulum.

So far, then, the available evidence proves that the cell-body is fibrillar and reticular. But the mere fact of this essentially reticular structure is not enough for us. Our sketch yielded us the definite, highly centralised organisation of the typical cell. The originally uniformly distributed network had been entirely rearranged. The chromatin scattered originally over the whole was for the most part gathered into a central tangle of the network, which took on a vesicular appearance, because a quantity of fluid associated with the chromatin filled its central meshes and pressed out its peripheral and more matted filaments. Round this felted "membrane" the rest of the network was specially arranged so as to radiate outwards as branching and anastomosing strands to the surface of the organism.

Repeating the argument urged in the last chapter,

I say that the chief effect of this complication of the network has been to advance the organism in the scale of efficiency. The organism and the environment have to be considered together. Life, indeed, consists of the power to respond effectively to environmental stimuli, attractive and repellent. The organism effectively responds to the former when it learns how to utilise them for its own well-being, and to the latter when it successfully resists or escapes from injurious impacts. If we apply this to our evolution of the protoplast, we can easily see that if the chromatin is needed by the linin network for the expression of its energies, its concentration at the centre where it is most accessible from all parts of the surface is an absolute necessity for perfect efficiency; the radial arrangement of the filaments is also necessary in order that their energies of contraction, nerve conduct, and conveyance of material may be brought most rapidly, directly, and fully into play.

Turning again to the so-called cell-body, that part which surrounds the nucleus and comes into most immediate contact with the environment, we have to show that this not only has a fundamentally reticular structure, but that the reticulum is arranged in the manner assigned to it in our sketch, in spite of the fact that it generally has the appearance of a more or less homogeneous mass of matter, unless the filaments happen to be beaded with chromatin or other visible substances.

Now, in the first place, if the essential structure of these elementary organisms is a network of such morphological and physiological importance that its threads are the paths along which its energies flow outward and the stimuli from environmental impacts

inward, then it is to be expected that traces of such filaments would show in some way at the surface, especially when we remember the yielding and semi-fluid character of the substance itself. Again, if traces of radiation show where the surface is hard, these may be claimed as striking instances of the synthetic activity of the underlying and invisible rays. Here we have overwhelming evidence; for they do show at the surface, and a comparative review of the many ways in which they appear as cilia, rays and flagella is most significant and instructive.

Either cilia or rays are almost universally present in elementary organisms. The cilia are, for the most part, organs by means of which an immense amount of energy is visibly expended at the surface; and their structure is such as to favor our theory. It is obvious that they may originally have represented the outermost fringes of a uniform chromidial network. Their roots can even now be traced into the interior in many organisms.¹ They have been seen to join the meshes of a network directly, sometimes to run inwards as apparently isolated strands to the nucleus, or else, *e.g.*, in multicellular organisms, to unite into bundles and to run past the nearest nucleus into some deeper layers of the network. These variations are very instructive, for they may mean either that the fundamental filaments, the tips of which run out into cilia, are actually progressively isolated so as to connect them with some deeper centre, or that the streams of chromatin necessary to the display of their energies are being concentrated and confined to particular paths, thus rendering those

¹ The evidence for this statement will be found farther on (p. 95, Fig. 16). We must be content here merely to indicate the fact, reserving its discussion for a while.

special conducting filaments visible. The isolation, in this latter case, would be functional and not necessarily structural. While these are points that must be left to be unravelled by future research, we are, in either case, supplied at the outset with an illustration of the progressive centripetal differentiation referred to above as one of the laws of the evolutionary process. In further confirmation of our main point, the essentially filamentous structure of the cell, another fact may be added to the many actual observations connecting cilia with a filamentous network. In some cases where the process of cilia formation has been traced with great care in small plant organisms, the nucleus, which I regard as a special tangle of the network, has been seen to move toward the outer wall and cilia have appeared apparently from it or from the spot where it touched the wall.¹

Now these facts are of the very first importance for us. I feel justified, indeed, in claiming that cilia, wherever found, are, in essence, the fringe of the outermost filaments of some continuous reticular system underlying the organism. But we could not say, from the presence of cilia alone, what degree of differentiation the reticulum has undergone. These organs might represent the free ends of filaments of a uniformly distributed network of the most primitive type, or they might be the protruding ends of bundles of filaments functionally or actually isolated² and coming to the surface from some deeper centre.

But, while it would appear that cilia might be found

¹ See Strasburger's *Histologische Beiträge*, Heft vi, p. 182.

² This distinction between functional and actual isolation of the fundamental filaments will occur again in connection with the development of the nervous system.

in any condition of the fundamental network, rays, streamers, and flagella almost certainly betoken some degrees of differentiation of the arrangements of its strands. The fact that the characteristic movements of rays and streamers are radial extension and contraction round the nucleus, of itself suggests some kind of radial rearrangement of the reticular filaments.

A flagellum may be considered as one single specialised streamer. Indeed, the direct connection between this and the nucleus has long been observed, and there are reasons founded on observation for believing that it is a drawn out portion of the network, like a streamer. That the streamers are protrusions of the network as a network we know from Bütschli's beautiful figures of the protrusion of the great single stream of *Gromia*.¹ This arrangement in *Gromia* must, however, be regarded as secondary and due to the development of a shell; it is only referred to here in order to show the essentially reticular structure of the protoplasm itself.

The terms cilia, rays, flagella, were necessarily, in the first place, descriptive and had no reference whatever to the network, the existence of which was, at the time, unknown, and we cannot now make these terms fit into any scheme based upon reference to the fundamental network. There are small and large cilia, small and large rays, small and large flagella. What is called the flagellum of a Microbe, *e.g.*, of a *Spirillum* or of a Bacterium, might well consist of one single linen filament, just as the larger cilia might be due to the protrusion of small groups of such filaments. At the same time, it must be remembered that the implied

¹ *Investigations on Microscopic Foams and on Protoplasm*. Engl. Tr. by Minchin, 1894. In Fig. 3, p.43 the reticular character of the retracted streamer is clearly visible.

distinction here made between cilia and flagella, viz., that cilia may generally be regarded as so many single filaments of the external fringe, while a flagellum or a streamer is a distinct prolongation of a portion of the reticulum itself, is hypothetical. As a matter of fact, we do not know what the real fibrillar arrangement within the cilium is. I am often driven to think that even the smallest cilium contains a number of the fundamental filaments. The usual view that these are all modifications of the pseudopodia of an *Amœba*, and, therefore, fundamentally homologous, is quite unnecessary, and, as we shall presently show, very improbable. The point is of some importance for our case, for a strong argument for our theory can be drawn from the fact that these primitive protoplasmic organisms show so many independent filamentous peripheral organs referable to different specialisations of the essentially filamentous texture of the organisms themselves. We shall return to the pseudopodia of the *Amœba* later on but, in the meantime, let us advance from these active organs to gather further evidence from the various shells and outer coverings which, though passive, are also peripheral organs.

The obvious notion once prevailed that shells and outer coverings were due to the direct modification by air or water of the outer layers of the living substance. The surrounding medium must, of course, affect the surface to some extent, *e.g.*, exposure to air causes evaporation. But such direct modification is quite inadequate to account for the phenomena.

It is certain that the beautiful shells found among the protoplasts are due to some active principle in and essential to the organism itself. The details of this principle will be more fully discussed below; our chief

concern in this connection is to point out how common are radial skeletal structures or textures. No matter what material the skeletons are made of, these traces of radiation appear with such persistence and in such variety that it is hardly possible to doubt that some

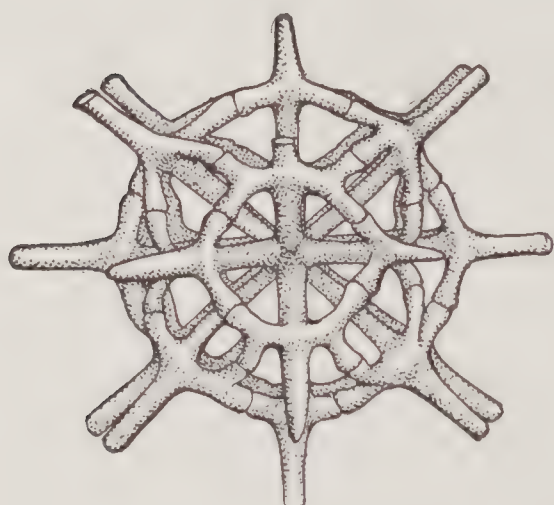


FIG. 2

A Radiolarian (*Phractaspis prototypus*, after Haeckel from Lang's "Text-book of Comparative Anatomy," Pt. I), showing the radiate character of the skeleton.

subtle radial system is an essential factor in the structure of the organisms. Fig. 2 is of a Radiolarian, and thousands like it might be reproduced showing radial structure, while in Fig. 3, a portion of the shell of a *Gromia* is shown with a fine radiation in its texture.

Now it is obvious that, if our theory is correct, the cell or protoplast has the reticular structure above assigned to it, and, if the filaments are endowed with synthetic functions and can carry materials to the surface, then we have an instrument at hand which will enable us to sketch a fairly intelligible scheme for the co-ordination of all these marvellous forms as in every case due to the activities of the organism. This we shall attempt in its right place. At the present moment it is enough to have shown that these passive organs of protection promise to be witnesses in our favour, not only as to the essential reticular structure of protoplasm, but as to the radial arrangement of the network round the nucleus and the essentially synthetic powers of the strands themselves.

Passing on from the better known peripheral organs

of the protoplasts, and their protective coverings, which bear witness more or less confirmatory to the existence of a fundamental filamentous or reticular texture of at least the outer layer of these organisms, there are two more organs to be mentioned and these are the most remarkable of all. I refer to the organs possessed by

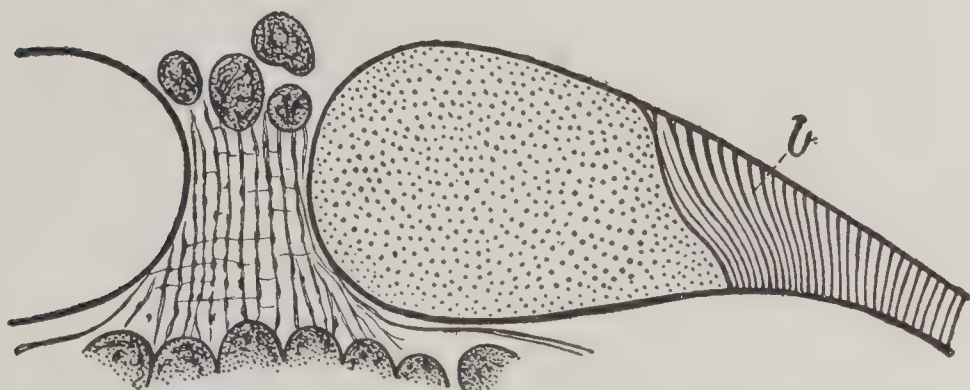


FIG. 3

Shell of *Gromia Dujardini* (after Max Schultze, from Bütschli's "Protoplasm and Microscopic Foams"): *b*, the portion of the shell which is radially striated in optical section. The retracted protoplasm in the opening of the shell has a very distinct radially fibrillar structure.

many of these simpler forms of life for the ejection of filamentous darts. These, when found in the more primitive protoplasts, are called "trichocysts," and when occurring on a larger and more complicated scale in primitive metaplasts, "nematocysts."

It is clearly possible to regard the trichocysts as small portions of the tips of some of the fundamental filaments coated with elastic substance and, thus coated, imprisoned in such a way as to cause them to dart out when released. Possibly the dart itself is merely the elastic sheath from which the living filament has withdrawn. If so, we may further imagine that, in the act of withdrawing, the filament filled the hollow where it had been with some poisonous matter. But

these are secondary speculations. The three points which for the moment interest us here are: (1) That these weapons are filamentous; (2) That the reticular structure of the organism makes it possible to understand their development as a very natural armature for an organ with such a texture; and (3) That our principle of skeletal formation enables us to account for them as discharges of waste matter brought to the surface by the filaments. These are clear gains.¹

Now, there is no difficulty at all in the appearance of many different kinds of filamentous organs at the surface of cells if we regard them all as so many differentiations of the surface of the fundamental network; given the filaments with their interesting physiological characters, we should expect that they would appear at the surface for many and various functions, regarded as so many different responses to the stimuli of the environment.

Passing on now from the cell-body or the peripheral portion of the organism, we come to the nucleus. The filaments of its network are not obscured by being embedded in granular cytoplasmic matters, as are those of the cell-body. Its reticular structure is an accepted fact; the network can be seen with any good microscope and many of the details of its distribution can be made out. It presents a system of exquisitely

¹ Essentially the same method of explanation of the mechanism can be adopted in the case of the nematocysts of a *cœlenterate*, only these larger stings are certainly not composed of single filaments, but rather of strands of the fundamental network itself. Another instance, less well known but equally remarkable, is afforded by the common Teasel, in which certain gland cells are seen to protrude exquisitely fine filaments, for the passage of which no pores can be found in the cell membrane. The functions of these filaments are unknown, but they can contract and expand again, and seem to undergo very fine vibrations or tremblings.

delicate threads, a larger or smaller portion of which is made visible by being coated in varying degrees of thickness with the densely staining chromatin.

We have thus a subtle fibrillar network in the cell-body surrounding a fibrillar network in the nucleus, one network, therefore, embedded in another.

Now, *a priori*, one would say that these two reticular or, at least fibrillar, systems must almost, in the nature of the case, be continuous with one another, and the more important they are structurally and physiologically the more likely would this appear. But this apparently obvious conclusion has not been drawn, first of all because there was no certainty as to the existence of any fibrillar structure of the cell-body; secondly because, even if such a system exists, the nuclear membrane comes between and the appearances certainly suggest that the nucleus is a separate organ embedded in the cytoplasm; and thirdly, because many eminent observers who specially studied the point have emphasised the fact that, search how they would, they failed to find any connection between the fibrils of the cell-body and those of the nucleus. Let us try to meet these objections.

We may obviously pass over the first of them and deal directly with the nuclear membrane. We gather from Professor Wilson (*op. cit.* p. 38) that "the most probable view as to the origin and structure of the nuclear membrane is that long since advocated by Klein and Van Beneden, that the membrane arises as a condensation of the general protoplasmic substance and is part of the same substance as the linin network and the cytoplasmic meshwork." Now, according to our theory, the linin network within the nucleus and the cytoplasmic meshwork outside it are fundamentally

parts of one and the same reticulum, though possibly coated over with different substances. If, therefore, this early view is correct, the nuclear membrane is what our evolutionary sketch requires, a felting of the threads of the protomitotic network.

The most convincing observation confirmatory of this view of the origin of the membrane was obtained by me from the retina.¹ In some cells, the felting was seen opening out so that the intra- and extranuclear networks ran into one another without any apparent interruption. If this dissolving of the feltwork can be established, the question as to the fundamental continuity of the whole is finally settled. But is it not already established? Is not one very significant instance of this opening out and disappearance of the membrane already well-known? When the fibrillar system is re-arranging itself preparatory to nuclear division, the so-called membrane simply disappears, a disappearance which is specially significant since, as we shall see in Chapter XIII, the filaments of the network have to assume a radial arrangement before division is possible and, naturally, any special feltings of them would disappear at such a time.

It is essential to the protomitotic theory to be able to show that the nuclear membrane is a secondary felting of the originally diffused network which not only does not separate the intranuclear from the extranuclear reticulum, but in reality links the two together into a continuum. I may, therefore, be allowed to repeat and to strengthen the argument that it would be strange indeed to have one small network, the filaments of which are of essential structural and physiological

¹ See "Studies in Retina," Pt. vi, p. 318. Fig. 12.

importance, embedded in another (that of the cell-body) with no fibrillar connection between the two. This argument becomes much stronger when we turn to the metaplasts and find that, in them, the reticulum runs as a continuum throughout the whole organism. Is it at all probable that the nuclei would be small scattered networks embedded in and yet isolated from the main reticulum, especially since, according to the almost unanimous opinion of biologists, they are co-ordinating centres? The co-ordinating centres would, in that case, be cut off from organic connection with their spheres of influence if, as we maintain, the filaments are the structural elements for the contractile, nervous, and synthetic energies of the organism.

One would, therefore, be justified in dogmatically asserting that the networks of nuclei and of cell-bodies must form parts of the same system, even though no connection could actually be demonstrated, and the fact that it has been seriously denied is what we have to account for. Looking back, indeed, at this denial, it seems to me that it will prove not the least interesting chapter in the history of the cell doctrine.

So far as I have been able to read this story, a continuously increasing number of observations by leading biologists,¹ foremost among whom I may mention Frommann, were actually demonstrating connection between the network of the nucleus and certain fibrils coming in from the surrounding tissues which, for all practical purposes, may be regarded as those of the cell-body. These observations accumulated up to the eighties. But, since that time, until quite recently, all such connection has been emphatically denied.

¹A few of these will be mentioned in Chap. X., pp. 181-187.

The details belong to other chapters in which the tissues especially concerned will be discussed. I can only here tell the story in outline and clear the air by suggesting a solution. After studying the figures and reading the papers of the earlier observers, I was for a time entirely at a loss to conceive how this change of front could be accounted for. For, be it noted, other observations by these same early workers have stood their ground, though perhaps interpreted differently, and why should this one, which was not only correct but so probable in itself and so little likely to be misinterpreted, come to be now, for over twenty years, systematically denied? Strange as it may sound, in view of the advances made in microscopic technique, the reason can only be that later observers *failed to see* what the earlier observers saw. Indeed, cases are recorded in which the same observers failed later to see what had once been clear to them. It sounds most improbable, almost mysterious, as if recent observers had been suddenly smitten with blindness. And yet it may have the following very simple explanation.

It is obvious that, when the visibility or invisibility of such exquisitely delicate filaments depends upon the variations in the physiological condition, that is, in this case, upon the presence or absence of fine streams of chromatin granules or of chromatin combinations, there is abundant room for accident. An observer may announce the discovery of visible filaments radiating from the nuclear membrane because his material happens at the time to be in a favorable physiological condition. Nothing would suggest doubt as to this matter of visibility, the filaments were asserted to be there, if seen, or not there, if not seen. Hence, when the same tissue was re-examined, treated perhaps in

the same way, and the filaments were not found, the natural conclusion was that they did not exist and that what was first observed must have been an artifact. And, now, to this element of chance as to the physiological condition of the material, is added another which is artificial, namely that invisibility may be induced by the chemicals used in the preparation of the material causing the sudden complete retraction of the chromatin back on to the nuclear membrane; it is clear that if such chemicals came into general use, the recognition of the fibrillar connection of the nuclei might be put off indefinitely. I feel justified in suggesting that this is the real explanation of the extraordinary fact that whereas, thirty years ago, before the use of osmic acid became general, observers were on the highway towards realising the essential unity of the reticulum underlying both nucleus and cytoplasm, they were all turned off the track, and the discovery of the protomitomic network put off until now.

My own experience of osmic acid as a fixative supports this suggestion. It is most excellent for all ordinary work, but, however rapidly it fixes the material, it is not rapid enough to prevent all movement of the chromatin upon the linin filaments. It is not rapid enough, for instance, to prevent small streams of chromidia, which might be leaving the nuclear membrane and travelling outwards, from shrinking back, so that the filaments which were, for the moment, made visible became instantly invisible. In this way it is clear that a great variability in the visibility of the filaments radiating from the nuclear membrane might be expected. There would be natural variations due to physiological conditions and artificial variations due to the effect of shocks, some perhaps nervous, others,

as suggested, purely chemical. Certainly, the synchronism between the use of osmic acid and the period of persistent and authoritative denial of all fibrillar radiation from the nucleus is a matter worth investigating.¹

Be this as it may, the all-important problem as to direct continuity of the filaments of the nucleus with those of the surrounding network has now been set finally at rest by actual observation, not, however, in protoplasts, but on the tissues of a metaplast. In the chapter on the retina, we shall describe nuclei from which filaments can be seen carrying away chromatin, and the process is specially clearly seen because the nuclei happen to be in a fluid matrix unobscured by granular matter. This is, however, anticipating; our immediate argument is that the orthodox cell has at least so much in common with the cell of our evolutionary sketch that both are networks, similarly differentiated in being divided, by a felting of threads, into two parts, the network of the central vesicle being in this way separated from a peripheral system of filaments running radially from its surface to the external surface. The organic continuity of the intra- and extranuclear portions of the cell network which is required by our sketch, will be supported later by further evidence.

We thus have evidence that the cell not only has an underlying network, but that that network has the arrangement required by our sketch. * We have seen (1) that micro-organisms still exist which reveal the network in a simple condition—chromatin granules

¹ Professor E. A. Minchin has found that osmic acid when used for siliceous Sponges has the effect of tearing the collar cells away from the walls of the flagellated chambers, in the centres of which they may be found heaped up.—Ed.

being found in all stages of progressive concentration, from nearly uniform distribution to aggregation into a typical nucleus; (2) that the earliest organs of locomotion and prehension (cilia, rays, etc.) and protection (shells) all show the fundamental texture of the organism to be filamentous and radially arranged round the nucleus; (3) that, considering the important part played by the filaments, the network of the nucleus, as the organic centre, must be continuous with the network of the cell-body. This last point, indeed, is essential to our whole theory.

CHAPTER IV

PRE-CELLULAR EVOLUTION—THE PART PLAYED BY THE CHROMATIN

IN this chapter I shall deal chiefly with the chromatin partner of the protomitotic network and try to discover its relations, distributional and functional, to the filaments.

According to our sketch, the first step towards the production of the perfected cell, after the multiplication of the chromidial unit had resulted in a uniform network with chromidia at the nodes, was the grouping of the chromidia so as to form larger clusters and granules, until, in the finished nucleus, a comparatively speaking immense mass of chromatin may be stored. In this process, the chromidia travel along the filaments, the arrangement of which becomes secondarily altered by the alteration that takes place in the positions of the chromidia.

Now there are several reasons for believing that the larger masses of chromatin of whatever shape which characterise the fully developed typical nucleus are actually built up of dense masses of minute bodies, presumably chromatin, to which we may rightly attribute some morphological value. For instance, when the chromosomes divide during nuclear division, chromidia-like bodies not infrequently come into view, thread-like chromosomes sometimes splitting up into

rows of such bodies.¹ That this is not always the case is of no consequence; the fact that it occurs at all is of profound importance for our argument. Again, masses of chromatin are sometimes discharged from the nucleus, in which case they invariably, sooner or later, break up into dense clouds of minute bodies like chromidia² which gradually disperse. If we can show that, in this process, they always travel outward along the filaments of the network, we have a reversal of the gradual inward migration which preceded the evolution of the cell nucleus. The original movement inward, however, involved a corresponding rearrangement of the network, while these later outward migrations are simply for the distribution of material and, consequently, of energy.

These movements of the chromidia, into some of the details of which we shall have to enter later, seem all to hang together. If, from a primitive condition in which they were scattered on the threads of an undifferentiated network, the chromidia were gradually concentrated for the storage of energy in the most accessible position, *i. e.*, into a special central tangle, we should expect that they would be able to reverse the process when required for functional activities at or near the surface of the organism. We should expect this, that is to say, if once we had grasped the physiological importance of this substance, as shown by the now well established facts: (1) that if one of these primitive organisms is cut up the portion of it containing the nucleus alone

¹ Wilson, *The Cell in Development and Inheritance*, p. 244, Fig. 120 B and C.

² See below on the formation of the yolk and on the origin of the Nissl's clumps in ganglionic cells, pp. 59 and 210.

survives¹; and (2) that chromatin can be seen to be used up during functional activity.²

The prevailing doctrine that the chief importance of the chromatin is morphological rests mainly, I expect, on its remarkable behavior during nuclear division. Its movements are then so striking and yet so mysterious that they have naturally attracted an immense amount of attention. It has been called the "hereditary substance" of living matter, with the meaning that it is the essential substance which must pass from parent to daughter in order that the daughter may repeat the form of the parent. This claim, however, is only consistent with total ignorance of the existence of the underlying reticulum of linin threads, and naturally also of the intimate association between the chromatin and these threads. Indeed, it will be readily admitted that the scattered observations as to the chromatin were necessarily difficult to correlate into a coherent doctrine of its functions and importance, as also it was difficult to weave the scattered observations as to the existence of filaments of protoplasm into an intelligible whole. The protomitotic theory gives the reason for these failures. The chromatin cannot be studied with any profit apart from its indispensable partner, the linin network. Only when they are studied together can we arrive at any intelligible doctrine of either. The protomitotic theory starts with this intimate partnership as one of the fundamental facts of organic life. Why it should be so must ultimately be solved by the chemists. But our

¹ Verworn, *Allgemeine Physiologie*, Jena, 1895, p. 523.

² See Gustav Mann, *Jour. Anat. and Phys.*, 29, 1893, p. 100; also "Retinal Studies," pt. vi, *Quart. Journ. Micros. Sci.*, vol. 47, p. 337, and below, Chap. XII, p. 230.

sketch, starting from this partnership, seems to show that, of the two, the network is the more stable structural factor and the chromatin the more active chemical factor. The fact that the filaments are more especially the structural elements, only just traceable in the micro-organisms, becomes very pronounced in the larger organisms. In these, from the gradually increasing weights to be moved in larger and consequently heavier organisms, and the greater forces required for the reactions, the filaments come more and more to the front until, in what I have called the ergastic tissues, *i.e.*, the contractile and the connective tissues, the skeleton, and the nervous elements of the highly differentiated animals, they are by far the most conspicuous factors. The chromatin and the cytoplasmic matters necessary for purely chemical reactions are, on the other hand, most conspicuous in the metabolic and secretory elements. While revising the arguments, we have to regard these later developments of specially filamentous tissues as specialisations of earlier filamentous elements which had their origin in the first groupings of the chromidia during the pre-cellular evolutionary processes.

These facts and considerations tend to show that, however physiologically important the linin threads may be, the chromatin also plays a part as indispensable for the production of the activities of life. I contend, therefore, that we are justified in expecting that if the chromatin originally clustered into a central nucleus so as to concentrate all the available energy at the most convenient point where it could be drawn upon by any part of the organism, it would travel outward again to any point where it might happen to be required. We have, indeed, already seen evidence

of its travelling outward along the roots of the cilia, in whose vibratile energies it is used up.

In this discussion of the intimate association of chromidia with linin filaments, and, indeed, throughout the previous chapters of this work, it has been assumed that the chromatin travels along the filaments, almost as if in beads threaded upon them. We have now to advance one step further and to endeavour to establish this interrelationship by evidence. I hope to be able to show not only that the chromatin travels along the filaments but that it never normally leaves them until it passes off in combination with other substances as waste products or as secretions of various kinds. This may not admit of actual demonstration, but I shall now give some of the reasons which lead me to assert it until the contrary be proved.

Within the nucleus, the chromatin masses are always clotted upon the linin filaments or suspended as globules at the meeting points of several filaments. Outside the nucleus, I have not, in any instance, seen the chromatin free of the filaments however far away it may be, *e.g.*, in the rods of the retina at a considerable distance from the rod-nuclei (*cf.* Figs. 31 and 35, pp. 206 and 224).

Bütschli's statement that the microsomes and other granules always lie in the framework, never in the meshes of his foam structure, asserts the same thing in other words.

Large quantities of chromatin are frequently massed on the nuclear membrane and, since we regard this membrane as a felting of the reticulum, that is also so far corroboratory.

The different shapes assumed by the chromatin in fixed preparations (reticular clots and smooth

globules, are the most frequent) deserve closer attention. I say fixed preparations, for my own experience is that the sudden action of the chemicals may lead to a sudden shifting of the chromatin along the threads which, in some cases, appears to be of the nature of a shrinking together though, in others, the opposite effect may be produced. It is possible that the position of the chromatin may at times be such that the sudden stimulus fails to bring about any visible change of position or form. Be this as it may, the fact remains that, in all preparations, the shapes and distribution of the chromatin masses, large and small, indicate without exception their possible association with filaments and not seldom with filaments arranged as a reticulum.

Such an association of chromatin and filaments in the form of shapeless clots or smooth globules within the nucleus is well known (see Fig. 31, A-D). These differences of shape are probably to be referred to the different chemical and physical conditions of the individual masses at the moment, the varying conditions doubtless affecting the way in which they cling to the fibrils. The proportion of masses which take the one form or the other appears to vary in different nuclei; perhaps at different times with the different physiological phases. I have seen nuclei in the shell-gland of *Apus*, the chromatin of which was distributed as refractive spheres evenly throughout the whole nucleus. All alike appear to consist of chromidia and are known to react differently to acid and to alkaline stains.

When these spherical bodies occur outside a nucleus they are called centrosomes, and this is an excellent descriptive name if it can be shown that they always occur at the centres of radiating systems of filaments.

Such radial systems may involve different sized areas of the network. The largest are those found connected with nuclear division. Fig. 4 shows such a system with one of these central bodies. I produce it here in order to show the arrangement of the rest of the chromatin distributed upon the rays themselves in

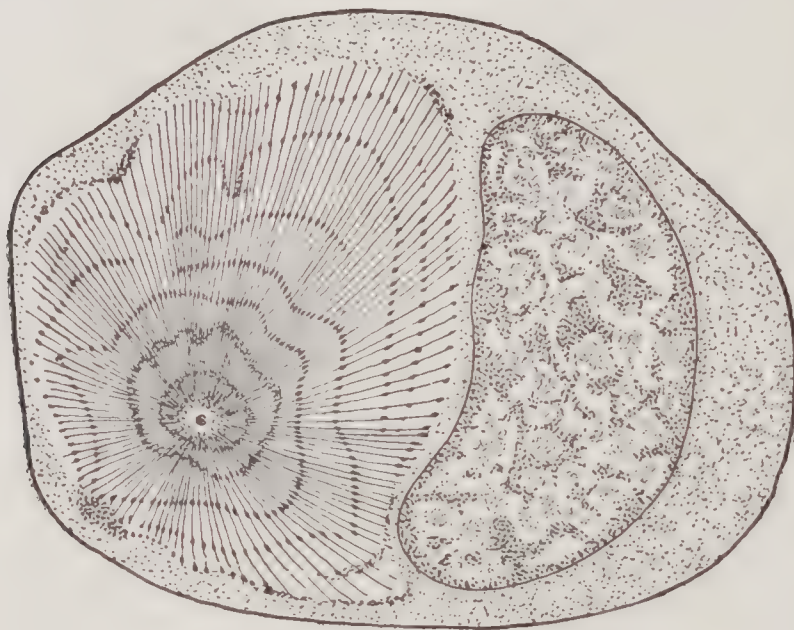


FIG. 4

Spermatogonium of Salamander (after Drüner, from Wilson's "The Cell, in Development and Inheritance"), showing a portion of the network arranged radially round a centre, and the particles of chromatin ("microsomes") arranged upon the filaments.

a way that certainly suggests that they are confined in their movements to the filaments, along which they can shift like beads to positions where they can find room. This bead-like arrangement is very suggestive and is so common under many different circumstances as to leave little doubt as to the correctness of the interpretation here given. Beads of chromatin can be seen running down the rods of the retina and, at times, rows of beads can be seen in the cytoplasm

round a nucleus where the cytoplasm is too dense to allow the filament to be seen (see Fig. 31, A).

The clinging of the chromosomes to the filaments of the spindle during nuclear division will doubtless already have occurred to the reader. This remarkable phenomenon suggested to some observers that the filaments were produced for the special purpose of pulling or pushing the chromosomes apart. Not less remarkable is the sequel; after division, the masses of chromatin in the daughter nuclei are all found still suspended upon the filaments after the rearrangement both of chromatin and fibrils. In Chap. XIII we shall see that the whole of the spindle figure becomes intelligible if we bear in mind that it is not only the chromatin which has to be divided, but the fundamental reticulum also, from which the chromatin cannot be separated.

As a further proof of the essential and inseparable association of the chromatin with the linin threads we have the fact that the chromatin does not necessarily leave the threads when combined with other matters. In many cases it does so but, in others, it remains as one of the essential principles in the architectonics of living organisms. The whole principle of skeletal formation which will be elaborated in these pages rests upon the fact that the skeletal matters coat the filaments, and the variation in skeletal systems is due to difference in the arrangement of the filaments, the material coating them, and the way it is disposed.

The process of the formation of yolk in the egg affords another instance. I followed this out some years ago in examining thin sections of the eggs of *Apus* at different stages in their development. I became convinced, though without at the time fully appreciating

what I saw, that the yolk discs were threaded on the filaments of a network. At the centre of each disc was a minute staining granule round which the discs were built; focussing up and down, it was always possible to follow the thread out of the disc on each side for a short distance. In younger stages, strands of the network, unobscured by the multitude of developed yolk discs, could be seen radiating from the nuclei; near the nuclei these were thickened with deeply staining matter, but gradually thinned away along the branchings and anastomosings of the strands towards the periphery. In this I saw what appeared to me at the time, and what I now know was, a dispersal of chromidia from the nucleus throughout the body of the egg. Round these separate chromidia, when sufficiently spaced, yolk discs were formed and, consequently, were threaded upon the filaments.

On comparing this with the recorded observations of yolk formation, I soon found that the minute central granules were well known under the name of "lecithoblasts." They hardly need a special name, for they are apparently simple chromidia round which certain materials of the matrix slowly aggregate.

It is well known that, in some forms at least, the initial step towards the process of yolk formation is the appearance of a thick cloud of chromidia which look as if they had just left the nucleus. While still congregated together, the mass is known as the "yolk nucleus."

I do not remember finding any trace of such a definite cloud of chromidia in the eggs of *Apus*; the chromidia left the nucleus in dense outward streams along the branching, radiate strands of the network. But these are not important variations; the one necessary point

is that the chromidia disperse along the filaments. The current doctrine, however, seems to be that the yolk granules lie in the meshes of the cytoplasmic reticulum and not upon the filaments. Now I do not know whether this doctrine rests upon actual observations or whether it is simply a natural though erroneous inference. In the former case, the question arises whether the cytoplasmic reticulum seen between the granules represented the real linin reticulum and not rather the intervening strands of perhaps coagulated plasmic or matrix material. If strands of the true linin were actually seen between the yolk discs, they may have been strands carrying on other functions and not producing or supporting yolk discs.

In any case it is clear that there is nothing in the current account contradictory of the account here given. Indeed, so far as it goes, it supports the protomitotic theory, inasmuch as it describes countless granules of chromatin leaving the nuclear storehouse to help in the formation of yolk granules. All that the protomitotic theory has done is to introduce the fundamental reticulum to an active share in the process. It must be admitted that this introduction gives a new meaning to the whole process, inasmuch as the network, continuous throughout the whole organism, supplies us not only with paths but also with an active force for the gradual and even dispersal of the granules from within the nucleus outward and throughout every cell. Indeed, this particular case is very instructive because the chromatin, in forming the combination called yolk, not only does not leave the fibrils at all, but builds upon them a storage product which will sooner or later be needed on the fibrils

when they start growing round the periphery in order to develop into an adult.

Another kindred case, showing the intimate association of the products of metabolism with the fibrils, is supplied by certain chromatophores, as the largest

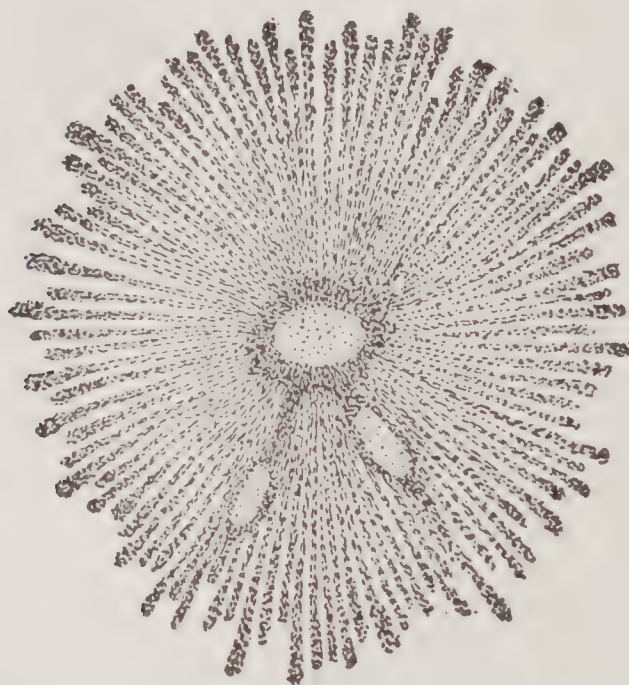


FIG. 5

A Chromatophore or pigment cell of the Blenny (after Zimmerman, from Wilson's "The Cell, in Development and Inheritance"). The pigmented granules are seen arranged in radiating lines which are recognised as homologous with the lines shown in Fig. 4. The pigment granules are therefore in intimate association with the protomitotic filaments.

pigment-bearing "cells" in the skins of many animals are called. These are known to be highly contractile, which, in itself, is a clear indication of the presence in them of the protomitotic network. Specially interesting to us are those cases in which the filaments are radially arranged, forming what has been termed

an "aster" with the pigment granules arranged along the rays (Fig. 5). Either these rays contract or the pigment granules, sliding inwards upon them, may be collected into a mass in the centre. In each case, the close association between the two is beyond question. But there is ground for believing that pigment granules are produced only in association with minute masses of chromatin; certainly the large grains of the eyes of *Apus* have centres which take chromatin stain, and I have seen, though but rarely, what I took to be a staining substance in the pigment grains of the mammalian retina.

This pigmented matter is not, like the yolk, needed for future purposes but, being a waste matter, finds its way eventually to the surface, always along the filaments of the fundamental network, as we shall see in the chapter on the epidermis. These, then, are cases in which the chromatin leaves the filaments in combination with other substances as waste matter.

Differing again from either the yolk or the pigment, we have the Nissl's clumps, which are clouds of chromidia seen emerging from the nuclei of large "ganglionic cells," spreading over the whole and eventually streaming away along the nerve strands. These will be discussed in the chapter on the nervous system; we may say briefly that, in this case, the chromidia travel along the filaments and are used up in the production of nerve energy.

Again, Montgomery¹ has described how hundreds of minute granules, "derivatives of the nucleolus," leave the nuclei in the subcutaneous glands of *Pisciola* and are used up in the formation of the granular

¹ "Comparative Cytological Studies," *Journ. of Morphology*, xv, 2; pp. 487-493.

secretion, thus again leaving the network altogether. In this case also, although he does not say so, it is certainly easier to think of the granules as moving along the reticular fibrils than as finding their way independently through the meshes. In one other case, however, this point, viz., that the chromatin granules do not leave the fibrils, is certainly implied. I refer to Hertwig's description of a starved Actinosphærium.¹ Almost all the chromatin wandered out into the cytoplasm as scattered "chromidia" and the *network on which they were suspended* was called the "chromidial network"—a term I have borrowed. Hertwig suggested that the process may be of morphological significance, being a return to the primitive diffused nucleus mentioned above. And this is in a measure correct, but so also is Calkins' suggestion that the "phenomena may mean nothing more nor less than excessive activity of *normal* vegetative processes, and may be without morphological significance."² The process is purely physiological; its morphological interest is limited to the fact that the wandering out of granules along the filaments is the reverse process of the gradual previous concentration described in our evolutionary sketch and resulting in a central specialised nucleus.

The case of Hertwig's Actinosphærium is of special interest because of the simplicity and completeness of its corroborative evidence. It not only shows us the wandering of the chromatin along the filaments but it shows us the chromatin being used and the supply in the nucleus, which is the central store, being ex-

¹ R. Hertwig, "Kerntheilung bei Actinosphaerium," *Jenaische Zeitschrift*, xvii, Id. 88.

² Calkins, *Ann. N. Y. Acad.*, xi, p. 379.

hausted; we presume that a good meal would replenish the stock.

These cases must suffice for the present; they not only establish the special points we are discussing, but, as all hang together, they take us back to the important question dealt with in the last chapter, where we endeavoured to show that the linin network within the nucleus must be continuous with the linin network of the cell-body. We can now add confirmatory evidence afforded by the movements of the chromatin. This substance, which is always found associated with filaments, travels along them from within outward, a state of things hard to imagine unless the filaments were continuous through the so-called nuclear membrane.

Of the mechanism by which chromatin alone, or chromatin in combination with other matters, moves along the filaments we as yet know nothing, but of its movement we shall continue in subsequent chapters to have abundant evidence. We shall find matters not only arranged but rearranged. The yolk, as we saw, after once being built up, is dissolved and used up in growth, and we shall find that even hard skeletal matters, after being deposited and after having functioned in one place, may be dispersed and redeposited elsewhere, as the exigencies of growth and of changing strains may require.

Before closing this sketch of the chromatin and its movements, evolutionary and functional, a sketch which has illustrated the impossibility of understanding either it or the filaments except in association with one another, I must briefly allude to a difficult subject. We have, I believe, in these last two chapters, seen enough to justify us in assuming that the chromatin affects the "chemical synthesis" (to adopt the words of Claude

Bernard), and the protomitotic network the "morphological synthesis," which are together necessary to enable us to obtain any insight into the phenomena of life. The very intimacy of the association between the two factors may have caused doubt to be expressed as to whether the chemical and the morphological syntheses were not one and the same process. It is difficult to understand how this could be the case, unless we assume a new vital force in what might otherwise be a purely chemical process, and there is no justification for such an assumption, since though, as we shall see in Part III of this work, there is reason for believing that all life processes have their concomitant psychical aspects if we could but recognise them—the physical counterpart must be analysable according to ascertainable physical laws.

But while such a distinction between the functions of the chromatin and the network may be useful and indeed, largely true, it is probably artificial. For the relationship between the chromatin and the filaments is certainly more than simply spatial and in all probability there are no chemical or morphological syntheses from which either of them is altogether excluded. The distinction is, however, useful and, in what follows, we shall find many instances, especially in the formation of skeletons, in which, though the chemical synthesis may not be actually traceable to the chromatin, the fact that the products are arranged in a manner traceable to filaments shows us quite clearly the important part played by the network in deciding the texture and form of the final result.

CHAPTER V

THE EVIDENCE AFFORDED BY WALL AND SKELETON FORMATION IN THE PROTOPLASTS

THE sculpturing of the shells of many of the primitive organisms has been claimed as evidence of some active principle underlying the process of wall formation, and the almost universal presence of radial striation, not only in the grosser forms but in the finer textures, as evidence for the radial arrangement of the filaments round the periphery. But the principle of radial formation could not be fully discussed until the travelling of chromatin and its combinations along the filaments had been dealt with, for the two hang together.

In the last chapter, several cases were given of the movement of chromatin and of the building up on the filaments of material compounds, but the persistence of this material upon the filaments to form protective coverings or skeletons was only alluded to, because skeletal formation plays such an enormous part in life and in the building up of organisms that separate treatment is needed to emphasise it. The skeletal formations of the protoplasts, with which alone we can deal in this chapter, may not seem to afford much evidence for our main argument, but when the same principle is applied to the skeletal formations of the metaplasts, the evidence is, to my mind, overwhelming.

We shall try to show that, from the beginning of life,

skeletons are due to the synthetic functions of the fundamental linin-chromatin filaments, and that, in any analysis of such skeletons, the radial arrangement of their texture is such as the cell resulting from our chromidial unit might have produced.

The first and most striking proof that coverings are



FIG. 6

The process of Cell-formation in *Reseda odorata* (after Strasburger).

built up by the deposition of matter at the tips of the filaments is supplied us by the plants.

Fig. 6 is so well known that little need be said about it. It does not represent a protoplast, but that makes no difference; it may be thought to represent a colony of individuals each of which separately might be regarded as a protoplast, a colony which presents us with a number of nuclei that have divided and moved apart, and now walls are being built up between them. These dividing walls first appear in the form of a row of granules in the equator of the spindle of filaments joining the nuclei. We here see the walls coming into being, and great quantities of matter massed near them. The exact process of the architecture is, naturally, not

shown; that process, or rather a provisional hypothesis as to its exact details, we shall be able to arrive at when we come to review the facts. Our first point is to prove that the filaments are essential factors in the process, not only in that they convey the material, but in that their arrangement conditions the arrangement of the wall texture.

Before passing on to this second point, let us note in this figure the radial arrangement of those portions of the fundamental network which surround the nuclear tangles. Even if this is not the normal phase, the latter is not likely to be fundamentally different. It is possible, indeed, that the radial arrangement, which seems so pronounced, may be due almost as much to the radial streams of matter moving outward towards the periphery and making certain filaments specially conspicuous as to any actual re-arrangement of the filaments themselves.

We thus seem to find, in the plants, direct and conclusive evidence that it is the protomitomic reticulum which plays the chief structural part in the building up of walls, and the material used seems to come in part from the nuclei. The association between wall formation and the nucleus which, according to our sketch, is but a differentiated portion of the protomitomic reticulum especially rich in stored-up chromatin, is further seen in the following observed facts. Haberlandt¹ has described how the nuclei in epidermal cells or energids move to the outer walls in order to thicken them and remain closely applied until this thickening is accomplished, then move away again. If the inner wall is to be thickened, the nucleus moves to the

¹ Cited by Wilson in *The Cell in Development and Inheritance*, with illustrations, p. 347.

inner wall, a fact which shows that the movement is not simply a reaction to external physical stimuli from air or light, but takes place for an express purpose.

In a description of cilia formation in the zoospores of *Vaucheria* also, Strasburger¹ has described the movement of the nucleus to the wall, which thickens at that spot, while round the thickened area the cilia appear.

Growth of the tips of root hairs, which also means necessarily the extension of the walls, has been seen to be associated with movement of the nuclei into the growing tip, the spot where a new growth starts being also determined by the proximity of a nucleus.

Still more startling evidence of the intimate association between wall formation and the filaments has been furnished by Townsend.² If long cells, like those of hairs, are plasmolysed so that the protoplasm breaks up into fragments, one of which alone has the nucleus, the non-nucleated fragments can secrete wall membranes for themselves only so long as they have retained fibrillar connection, however fine, with the nucleated fragment. This last most interesting fact not only connects wall formation with the filamentous network, but also shows that the reticulum may be stretched and pulled out of shape and still retain its functions. The significance of this fact cannot be gone into here, but it should be borne in mind. Here we are interested solely in the synthetic energies of the filaments, which include not only the conveyance of materials as just stated, but also, apparently, some impulse or "instinct" to dispose of those materials according to a definite plan.³

¹ *Histologische Beiträge*, vi, 1900, Jena.

² Cited by Wilson, *l.c.*, pp. 345-346; see also the same for kindred observations on the Protozoa, etc.

³ For a striking instance of this latter force see pp. 76-78.

Among animal forms we find much to corroborate what we have learnt from the plants, viz., that the filaments convey the materials for wall formation and deposit them in the positions required; in the protoplasts, apparently at the tips of the fringe. Whatever the origin of the material which united with chromatin to form the walls in plants, we may assume that, in animal life, the large amount of waste due to the more active metabolism of free-moving organisms certainly plays a part. When describing the original chromidial unit, I assumed that the materials absorbed by the organism from without were attracted by the central chromidium and the products of their reactions were carried outward with the latter along the filaments. The waste matters would travel outward towards the surface. We assumed that they there spread out like discs round the tips of the filaments and that these discs together formed a protective pellicle. Great quantities of material thus accumulating round the tips would form cylinders of waste matter, so that the whole surface would consist of a more or less compact layer of rods. If these remained soft, they might slide upon one another, and thus form a continuous but very flexible outermost layer. If, on the other hand, they became in any way hardened, by admixture of organic compounds such as horn or chitin in various proportions, or by minerals, carbonates, and phosphates of lime or silica, or by mixtures of these latter with the former, then rigid walls might be formed, these walls being compact layers of prisms when the material was mainly mineral. This is, I believe, the *fundamental principle* of all skeletal formation in protoplasmic bodies, as we shall see far more clearly when we come to deal with the skeletal systems of the Metazoa.

Let me take as an illustration the shell of *Gromia*, which is built of carbonate of lime (see Fig. 3, p. 43), and has a radiate structure, and which I am inclined to interpret as consisting of a compact layer of prisms, each with a canal running along its axis to the exterior, these canals representing the courses of the fundamental filaments round which the material was originally deposited. When the process of deposition is over and the prisms are compactly fused together, the filament can act, not only for the conduct of nerve stimuli from without inward, but also perhaps as a means of material exchanges with the medium. If the whole of the shell were dissolved away, the remains of these filaments would represent not cilia, but the essential filaments of cilia. For each cilium must be considered as one or more fundamental filaments covered with some pellicular matter which makes it visible by thickening it.

Does not this principle supply us with a possible explanation of the clear, glassy ectoplasm of the *Amœba*? May not this latter be pictured as a compact fringe of cilia in which each cilium is more or less thickly coated with some clear, glassy material, supplied by the metabolic processes of the living substance? This material may be thought of as a thicker layer of a pellicle similar to that which renders ordinary cilia visible. Instead of being so thin as to allow the cilia to form a fringe of free ends, it is so thickly massed round them that they together form a layer of rods arranged at right angles to the surface and in contact with one another. When we come to consider the coverings of the Metazoa, we shall find many reasons for this belief. In the meantime there are one or two considerations which lend it indirect support.

The extraordinary capacity possessed by this ectoplasm of enveloping a food particle or of rejecting solid waste without apparent break or tear in the surface would be explicable if the ectoplasm were, in this way, a compact layer of mutually clinging but really separate radial blocks. This appears to be the simplest conceivable structure which could let particles through and close up again behind, the simplest, that is, which could be produced from the factors at our disposal.

Again, this method of building up the ectoplasm would account for the growth of the layer by intercalation or intussusception, the new material carried into it by or along the filaments resulting either in the thickening of rods of matter already on the filaments or in the addition of new filaments, the ends of which become similarly coated.

The fact that fibrils have actually been seen running radially into the ectoplasm leads naturally to the conclusion that such fibres must be rooted in a fibrillar system of the layer itself;—some continuity of texture may safely be postulated between adjacent tissues exhibiting such intimately co-ordinated relationship as the ectoplasm and the endoplasm of an *Amoeba*.

When the *Amoeba* encysts, the radial filaments become evenly contracted in all directions as a condition of rest, and the covering is consequently spherical and hard. The hardening may be due simply to density, or to the intussusception of some new material brought by the filaments. The movements of a flexible organism are simple and may be described as mainly centripetal and centrifugal, that is, as a bulging out or a drawing in of bent processes. That small, very sharp pseudopodia occur in some *amœbæ* might well be expected from the structure of the ectoplasm here

suggested, but they would not be true cilia, nor even transition forms between pseudopodia and cilia, the latter being specialised vibratile organs.

The view that the various peripheral organs of the protoplast can be accounted for as so many specialisations of the pseudopodia of the *Amoeba* of course practically assumes that the ectoplasm of the *Amoeba* is the primitive covering of living matter and that its protrusions are capable of producing all the peripheral locomotory organs of the protoplasts. Given a fundamental network, radially arranged round the nucleus, we are able to analyse the whole series of structures in a much more intelligible manner, as all being independent specialisations of filaments or groups of filaments of this network. The vibratile cilia are a peripheral fringe of such filaments or groups of filaments coated thinly over with pellicular matter; flagella are protruding portions of the network, portions definite and fixed and specialised for definite active functions. Streamers are indefinite protrusions. Pseudopodia are indefinite protrusions somewhat restrained by the thick skeletal covering, the ectoplasm, which is built round the periphery of the network out of waste matter, perhaps as so many rod-like masses upon a radial fringe. Trichocysts may also be coiled-up thread-like accumulations of waste matter formed on the ends of the peripheral filaments. I claim that this analysis is far more suggestive than the ordinary doctrine that all these peripheral structures can be referred to specialisations of the pseudopodia of the *Amoeba*.

But, while inclined to regard the ectoplasm as practically a layer of cilia which are not free, but turned into a compact and continuous covering by the accumulation of waste matter upon them, we must

not forget Bütschli's evidence, which shows a network permeating the whole of the ectoplasm, that is, a condition that would preclude the possibility of there being a free outer fringe.¹ The two views may be made to coincide if only the radially arranged portions of the Bütschli network are coated with the blocks and still form together a compact layer, although the blocks would not really be quite free, that is, they would not lose contact with one another, and would also be bound together laterally by the concentric filaments connecting radial and coated filaments. If these concentric filaments were elastic, that might help to explain the perfect closing together of the skeletal blocks after the passage of a solid particle.

Passing on now to the hard shells of the protoplasts, we find still further evidence in favour of the principle of skeleton formation by means of which we have sought to explain the soft ectoplasm of the *Amoeba*.

If the glassy rods of waste matter coating the tips of the fringe round the periphery of the network became impregnated with hard matters, lime salts or silicates, the rods, as they thickened and made the layer compact, would become solid prisms immovable on one another, and rigid shells would be formed. Such shells naturally require to have openings, otherwise the organism inside would be suffocated, and most hard shells have large openings through which the protoplasm can protrude and come into direct contact with the surrounding medium. In addition to these larger openings may there not also be minute openings at the outer tips of the hard prisms, openings through which the filaments running down the axes of the rods may

¹Compact layers of prisms are not rare in the formation of skeletal coverings.

protrude? We have already seen, in the case of *Groima*, a phenomenon which would bear this interpretation, and, in what follows, some evidence for believing that the rods are thus perforated from end to end and that the tips of the filaments must come through will be forthcoming.

In an organism surrounded by such a shell, we can imagine the waste materials still travelling outward along the filaments; if they are arrested within the shell, they will merely thicken it but, if they pass along the filaments through the prisms, they may deposit matter in various patterns on the outer surface. If these protruding filaments were themselves to grow in length and to become coated over with such hardened waste matter, we should get stiff rays ornamenting the shell. If, again, the filaments protruding from the tips of these stiff rays branched, and these branchings were coated over, it is clear that complicated reticular pattern might be produced.

There can, I think, be little doubt that some active principle is required for the production of the beautiful forms of so many of the skeletons of protoplasts, such as the *Radiolaria* and the sculpturing on them, and the protomitomic network enables us to account for even the most complicated of these skeletons (see Fig. 2, p. 42). Indeed, the *Radiolarians*, the great majority of which have reticular skeletons with many variations in the arrangement of the parts, seem to bear unmistakable witness to the existence of some underlying texture, which they express in silica. Fig. 7 represents such a shell composed of many concentric globes, each with its reticular pattern or fenestration. The protomitomic theory enables us to imagine it to be due to a periodical thickening of an original perforated shell by the

addition of a fresh silicate framework on the outside, in the way above described.

An attempt has been made to co-ordinate these Radiolarian skeletons with Bütschli's hypothetical foam structure of protoplasm, by supposing the walls of the alveoles to be perforated in various ways and degrees. However well this hypothesis appears at first

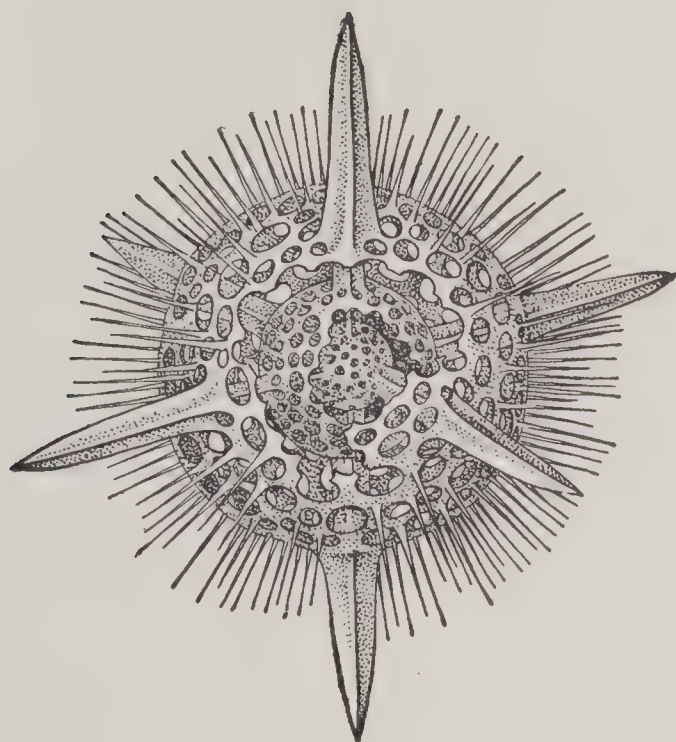


FIG. 7

A Radiolarian (*Actinomma asteracanthium*, Haeck.) the shell of which consists of three concentric fenestrated globes. Parts of the outer shells are removed to show the inner one.

sight to suit the case, it finds little support from any other skeletal formation, whereas the principle here laid down, viz., that skeletal formations are due to the coating with hard matters of the fundamental filaments of a reticulum, appears to elucidate the majority of the phenomena more satisfactorily.

If this reference of the beautiful regularity and sym-

metry of the Radiolarian shell to the ordered growth of the fibrils is correct, it presents us with a simple and instructive revelation of certain powers inherent in the protomitotic network—powers which pass beyond the range of explanation by any known law of physics. That, generation after generation, each kind should regularly reproduce the same pattern of shell requires some law of ordered growth to be acquired by each network, we may indeed say by every fibril, so that, as the network extends and its fibrils grow outward, they should do so in a pre-arranged order. This is the principle of heredity which runs through all organic life. Every reticulum repeats and will continue to repeat, for countless generations, the form of the parental reticulum, unless interfered with by some extraneous force from the environment. So far as we can see, the forms of life are due to the multitudinous interactions of this force of heredity, or tendency to exact repetition, with environments that are perpetually changing. (See further Chap. XIII, p. 264.)

We must now leave the pre-cellular evolutionary period and pass on to the next higher period, that of the cell itself. This, though more complicated, owing to the greater complication of its initial unit, will yet be found to yield abundant evidence in favour of our theory, and will, in the main, confirm the description given of the pre-cellular period.

CHAPTER VI

THE CELLULAR PERIOD OF EVOLUTION. DIFFICULTIES OF THE CELL-COLONY THEORY; ARGUMENTS FOR THE UNIVERSAL PRESENCE OF THE PROTOMITOMIC NETWORK

HAVING brought our sketch of the evolution of organic life from the stage of a hypothetical chromidial unit to that of the cell built up by that unit, we have now briefly to describe the new unit and to compare it with the other.

Like the chromidial unit, the cell is a radial system of linin filaments, but it is no longer a single system radiating from a single central chromidium; it is a complicated, anastomosing system radiating from a central tangle in which multitudes of growing and multiplying chromidia are stored, the whole (once more like the chromidial unit) being embedded in a fluid albuminous matrix.

This description shows us that the two units closely resemble one another, a point to which I wish to draw special attention. Both have centres of chromatin from which linin filaments radiate outward. The filaments, in both cases, transmit the chromatin itself to the surface for the production of energy at the surface, as, for example, for the vibration of cilia. In both cases, the materials absorbed from without tend to collect

round the chromatin centres (chromidia and nuclei respectively) while the synthetic products seem to travel outward along the filaments, either to be discharged at the surface or to remain upon the filaments as stored-up material or skeletal coverings, frameworks, yolk, etc. The filaments which are instruments for the specialisation and expression of the energy of the chemical reactions at the centre are, in both units, radially arranged so as to be able to respond to the impact of the environment at all points as speedily and effectively as possible. Further, the same organic principle is evident in the similar shape of the two units.

The cell unit is, however, higher than the chromidial unit in many significant ways. Owing to the large supply of chromatin stored in a central position in the organism and thus available for despatch to any point, the energy of response of the cell is much greater and, owing to the multitudes of anastomosing filaments, this energy can be used with much greater precision and economy. The greater number of radiating strands not only allows of greater vigour, but also of more perfect co-ordination of the reactions. Their number, also, allows of their being differentiated, some of them being specialised for contraction, others as nerves, and so on, and all are capable of more perfect adjustment so as to be able to respond to a far wider range of environmental impacts than was possible in the case of the simpler organism.

The life of the cell is thus made up of a vastly greater number of experiences than the more limited, monotonous life of the single chromidial unit, and, although the two units resemble one another in the machinery of their adjustment to the environment, the cell is a far more perfect machine. We shall see, as we proceed,

that evolution, which is complicating organic structure at this early stage, complicates it, not only here but always on a definite principle, viz., so that it may become more and more perfectly adjusted to respond to a wider range of environmental stimuli.

We have now to see how the advance from a minute protoplasmic unit to a metaplast took place. Evidently by colony formation but, in the case of the colony formation of the cell, as in that of the chromidial unit, we find a kind of mystery about the process, because biologists have hitherto failed to grasp the real structure of both units.

It was realised that the cell, as usually conceived, did not seem capable of growing beyond a certain very minute size, some egg-cells being the only conspicuous exceptions to this rule. Consequently, in order that larger and more complicated organisms might be produced, cells had to multiply and to form colonies. The cell was seen to multiply by dividing into two halves which again divided, producing four, and so on, until vast colonies of similar cells were formed. In some cases, these cells all moved apart, a swarm of protoplasts like the original cell being the result. In other cases, however, they remained together as an aggregate and in this way gave rise to larger and more complicated organisms. But, in this case, inasmuch as no satisfactory organic connection had been seen between the individuals of the colony, they were still thought of as separate, at least in the earliest stages when the individuals first began to multiply. In the adult, on the other hand, it is difficult to imagine that the cells were ever separate and distinct. *Here is the*

crux of the usual cell-colony theory. Facts pointed unmistakably to some original association which could justly be called colony formation, and yet no satisfactory principle of association was discovered which could bridge over the original separateness so as to effect the later union. Hence unicellular organisms of any size were always thought of as resulting from so many separate individuals, *in some mysterious way secondarily united.* These individuals of the colony are said to be able to influence one another, and to combine to build up highly complicated structures. One becomes modified in one way, another in another, as if inspired by some inexplicable instinct of harmony which enables all these modifications to fit together into an organic whole. Learned phrases are used which tell us nothing. It is said, for instance, that the special differentiation any particular cell undergoes in order to build up an organism is a "*function of its position.*"

This essential difficulty in the way of the cell-colony theory, as usually stated, cannot be better worded than it is in the following quotation from Professor Wilson's book.¹ Accepting the cell as the unit, he writes: "There is at present no biological question of greater moment than the means by which the individual cell activities are co-ordinated, and the organic unity of the body maintained; for upon this question hangs not only the problem of the transmission of acquired characters, and the nature of development, but our conceptions of life itself. Schwann, the father of the cell theory, very clearly perceived this and, after an admirably lucid discussion of the facts known to him,

¹ *The Cell, in Development and Inheritance*, p. 58. New York, Macmillan, 1900.

drew the conclusion that the life of the organism is essentially a composite; that each cell has its independent life; and that the whole organism subsists only by means of the reciprocal action of the single elementary parts. This conclusion, afterwards elaborated by Virchow and Haeckel into the theory of the 'cell-state,' took a very strong hold on the minds of biological investigators, and is even now widely accepted. It is, however, becoming more and more clearly apparent that this conception expresses only a part of the truth, and that Schwann went too far in denying the influence of the totality of the organism upon the local activities of the cells. It would be absurd to maintain that the whole can consist of more than the sum of its parts. Yet, as far as growth and development are concerned, it has now been clearly demonstrated that only in a limited sense can the cells be regarded as co-operating units. They are rather local centres of a formative power, pervading the mass as a whole, and the physiological anatomy of the individual cell falls into the background. . . . Broadly viewed, the life of the multicellular organism is to be conceived of as a whole, and the apparently composite character that it may exhibit, is owing to a secondary distribution of its energies among local centres of action."

With regard to this paragraph, we can only say that the difficulty between a colony of separate cells and an essential unity cannot be got over by words. The metaplast, if it is such a cell colony, is not an "apparently" composite body, but *is* a composite body, and its unity is incomplete and secondary. If, however, the metaplast is, as the protomitomic theory proclaims it to be, a unity, then its composite character is apparent

and secondary, but, in that case, the doctrine of separate cells falls to the ground, for we cannot keep the separate cell-colony doctrine and the essential unity of the metaplast side by side; they are mutually contradictory.

Here, as in the case of the colony formation of the chromidial unit, the whole of the difficulties vanish the moment the linen network underlying the visible protoplasm and accounting for the distribution of the chromatin is recognised as the essential morphological factor.¹ The problem is exactly the same as that encountered at the same place in the sketch of the pre-cellular evolution, that is the evolution from the chromidial unit to the cell. Its solution is the same here as it was there. The recognition of the filaments as single threads or as strands radiating outward from a central chromatin mass, chromidium or nucleus, enables us to conceive of the unlimited multiplication of the central mass with the accompanying filaments lengthening and longitudinally splitting according to their position with relation to the planes of division, so that, however many chromidia or nuclei are produced, they all remain connected as the nodes of a continuous network. The plan is essentially the same in both cases; it is only the details of the process that differ, being naturally more intricate in the case of the dividing nuclei than in that of dividing chromidia. It is a more intricate process because the central mass is no longer a single chromidium but crowds of chromidia aggregated together in various ways upon a central tangle of the filaments, and the radial arrangement arrived at does not consist of

¹ Indeed, had the filaments always been visible, I doubt whether the separate cell-colony theory of the metaplasts would ever have arisen.

single threads, but of a network of anastomosing strands.¹

According to the protomitomic theory, there is, during division, no rupture of any kind in the filaments, and no absolute and complete separation of the individuals. If, then, we are to apply the term "colony formation" to the process at all, it must be in the sense of a simpler and more elementary kind of colony formation in which the individuals do not separate. Such colonies are common enough in both the animal and the vegetable kingdoms. We recall the Bryozoa and the compound Anthozoa, in which the offspring bud from the parent and remain, throughout life, not only attached but in organic continuity. The vast majority of the more important plants are colonies of this kind. And this, on a lower level, was the type of colony formation which enabled the protoplast to produce the metaplast.

In pre-cellular evolution, as in this cellular evolution, the unit develops by simple growth—growth involving, for reasons which must be sought in the physical constitution of the elements themselves, successive divisions of the chromatin masses. The chromidial unit grew with successive doubling divisions of the chromidia which were then spread out upon a network of the filaments. And now again, the cell unit grows in the same way by successive doubling divisions of the nuclei which also spread out over a still more complicated network of anastomosing strands. This exposition is simple and clear,

¹ The process appears to me essentially the same but, on account of its intricacy and also on account of the special importance of any would-be clue to the mystery of karyokinesis, I prefer to postpone a discussion of the details till Chapter XIII.

but the real question is, is it correct? Can any evidence be brought forward in its favour? Let us see.

In the first place, the transition from the single protoplast to a colony of protoplasts seems to have been gradual; we do not have to jump from the

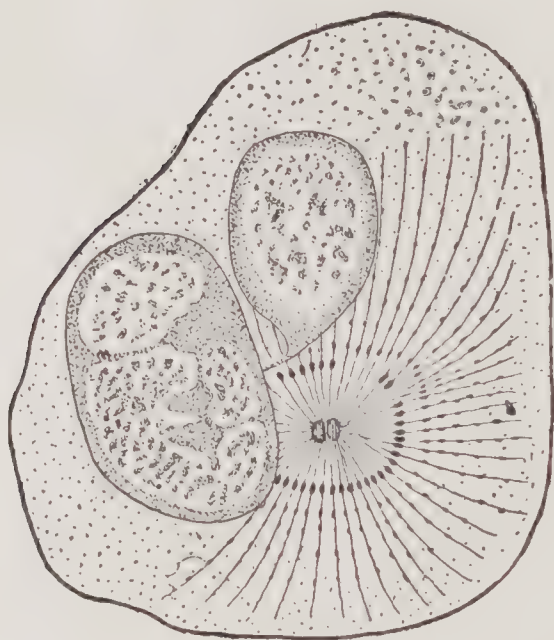


FIG. 8

A wandering cell of Salamander, with double nucleus (after Heidenhain, from Wilson's "The Cell, in Development and Inheritance"). The radiating fibres beaded with chromatin.

one to the other.

Starting from the hosts of simple, minute protoplasts, each with a single nucleus, we come to others larger in size, with the nucleus still undivided but showing what appears to be a tendency towards division (see, for example, Fig. 8), then a moniliform nucleus appears (Fig. 9) as if on the point

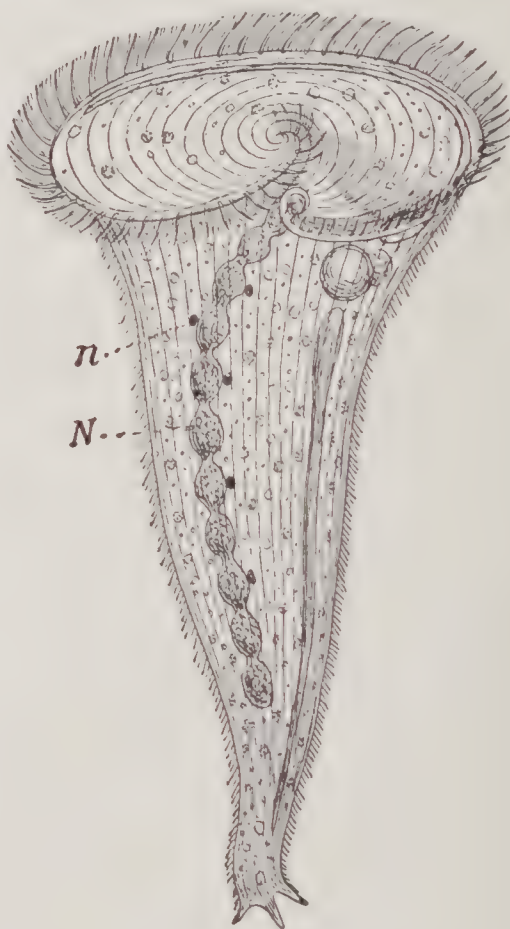


FIG. 9

A multinucleate Protozoan (*Stentor polymorphus*, after O. F. Müller, from Lang's "Lehrbuch der vergleichende Anatomie," 2d ed.). *N*, the moniliform nucleus; *n*, bodies called micro- or para-nuclei.

of breaking up into several nuclei, and next forms such as *Paramecium* (Fig. 10), which regularly have two distinct nuclei, one large and the other small, each apparently specialised for a different function. Still further advanced, we have forms with indefinite numbers of nuclei up to many hundreds (see Figs. 11, 12, and 13), but without visible traces of tissue formation. And these lead on to forms of still vaster proportions with thousands of nuclei and the beginnings of tissue and organ formation (see Fig. 14) which represents the young growth stage of the Sponge *Aplysilla sulphurea*.

With regard to variations in texture, we note that the small forms seem to be fairly compact and homogeneous, which we may assume to mean that the meshes of the reticulum are evenly distributed and generally filled with granular matter and show but few clear spaces. The larger forms (see Fig. 14) begin to show specialisation of the reticular structure which exhibits variations in the size of the meshes, these being smaller in some parts, larger in others, as if the filaments had run together here and there into strands with larger fluid spaces between them. This rearrangement into strands with large meshes might easily be a specialisation for more perfect co-ordination of the contractility and other elementary functions of the network, while the larger fluid spaces may have physiological advantages, probably circulatory, not needed by organ-

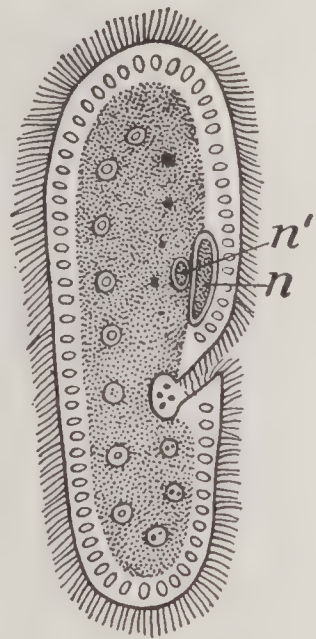


FIG. 10

Paramecium aurelia, a form with two distinct nuclei; *n*, the macronucleus, *n'*, the micronucleus.

isms of smaller size whose smaller meshes are filled with granular matter or whose circulatory needs appear to be supplied by a special pulsatory vesicle.

If we now compare the open reticular arrangement of the larger Infusoria with the similar reticular structure

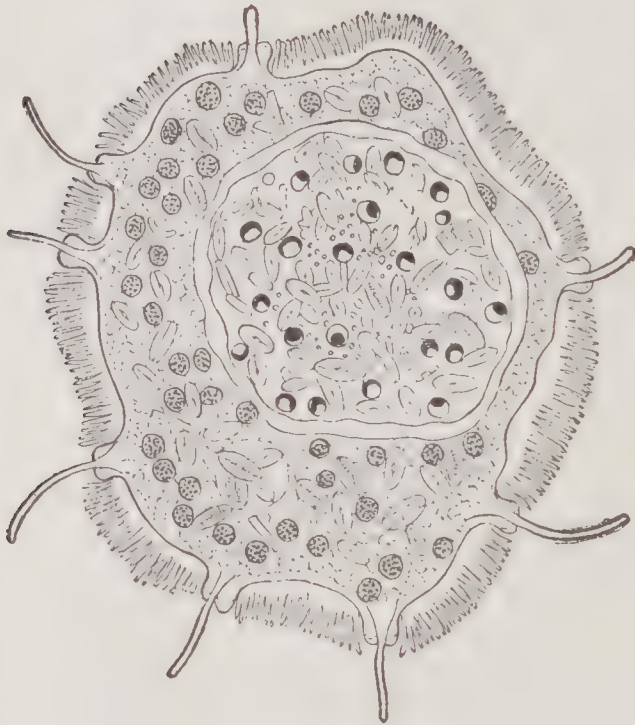


FIG. 11

A large multinucleate Protozoan (*Trichosphaerium Siboldi*, after Schaudinn, from Lang's "Lehrbuch der vergleichende Anatomie," 2d ed.). In addition to the nuclei and the ingested diatoms, a second individual can be seen also ingested; the character of the nuclei of the individual undergoing digestion is quite altered.

of a larval Sponge (Fig. 14), we see essentially the same texture except that, in the Sponge, the nuclei are numerous, separate, and distinct, and mostly have a certain amount of granular matter clinging to them and to the filaments which connect them. In *Stentor* (see Fig. 9), this matter is not attached to the nucleus, but this difference is altogether due to the physiological condition, the amount of granular matter massed round any nucleus being

simply a question of supply. In addition to these two conditions: that of the Infusorian, in which the matter is very scanty, and that of the embryo Sponge shown in Fig. 14 in which it is massed round the nuclei and runs out along the connecting filaments, forming stellate bodies, we have a third: that found in the egg, *e.g.*

of a Sponge (*Sycandra raphanus*) and in the earlier stages of the embryo. The store of matter in the egg is enormous (see Fig. 15) and, aggregated round the nuclei of the blastomeres in the 4, 8, and 16 stages, causes them to appear like a pile of separate spheres. That these are mere differences of condition we gather from the fact that, as the embryo grows, this pile-of-balls stage passes away. In an older embryo, the nutritive supplies, in so far as they are not used up, are more spread out (see Fig. 14). They no longer fill the whole of the space between the nuclei, except in the peripheral layer. Throughout the rest of the body, the stored matter is arranged in stellate masses round the nuclei in varying quantities.

But here let us pick up the threads of our present argument.

We have so far seen that organisms exist which show that the multiplication of the nuclei was gradual; that there was no sudden break from simple protoplasts to colonies but, on the contrary, a naturally ascending series from filamentous systems with one nucleus to those with many millions of nuclei. Gradual variation in the distribution of the filaments can also be traced even in these very earliest stages, the simplest uniform condition being departed from as the organism grows in size and as thicker and stronger strands are needed. As the organisms advance in complexity, specialisations

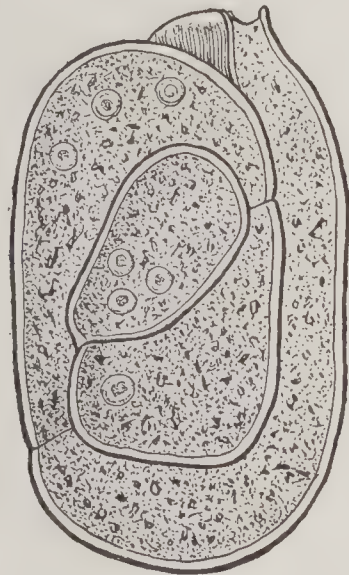


FIG. 12

A multinucleate Protozoan, *Millioli*, with calcareous framework (after Hertwig, from Lang's "Text-book of Comparative Anatomy").

of strands will be found to play an increasingly important rôle. And, lastly, we have very significant variations in the distribution of granular matter round the nuclei. This latter is a very important point, not

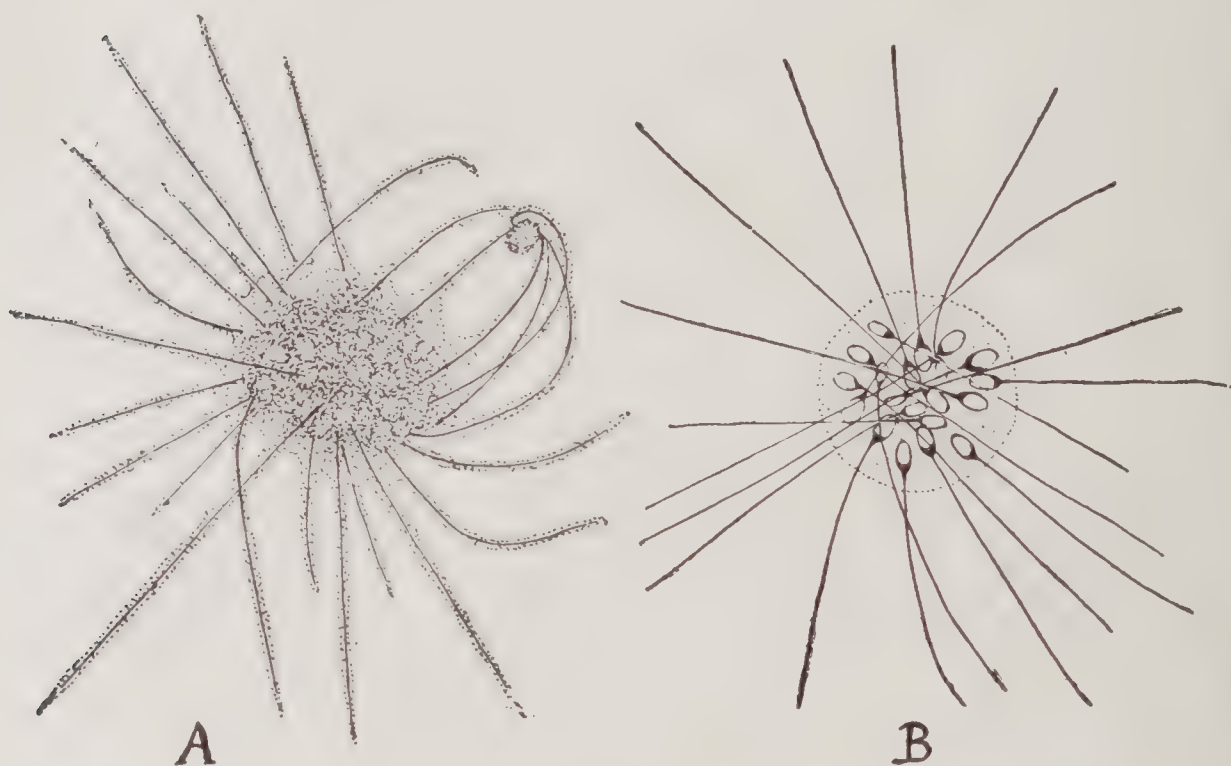


FIG. 13

A multinucleate Protozoan (*Comptomena nutans*, after Schaudinn, from Lang's "Vergleichende Anatomie," 2d ed.). B is a diagrammatic reconstruction to show the probable distribution of the nuclei and their relation to the rays. That these nuclei are all connected together we gather from the co-ordinated action of the rays in seizing the food particles shown in A.

so much for its own sake, but as illustrating the difference between the old theory and the new.

The essential elements, according to the old theory, were "cells," *i.e.*, masses of protoplasm, each with a central nucleus, cohering together so as to build up gigantic colonies. The manner in which this association took place in the earlier stages is unexplained, but in adult stages, of animals at least, ultimate fibrous connections between the cells are revealed

which make it difficult to imagine that they were ever separate.

The protomitotic theory claims that the fundamental substructure of all protoplasmic bodies is a continuous filamentous system with nuclei distributed as centres of functional activity, one sign of which

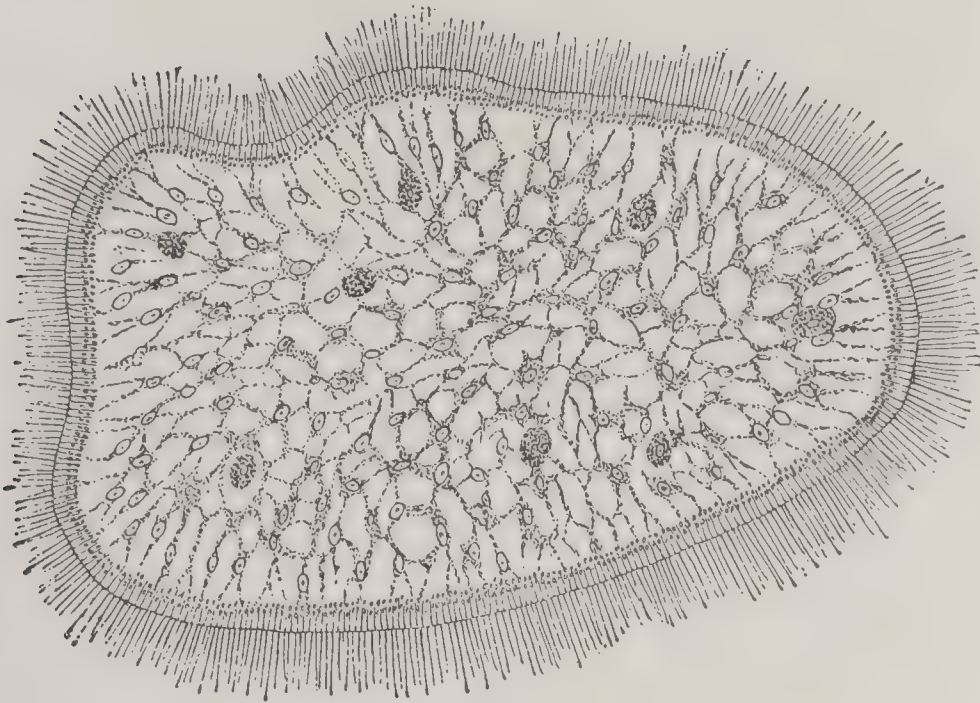


FIG. 14

A reconstructed section through the larva of a Sponge (*Aplysilla sulphurea*, after F. E. Schultze), showing the body of the whole animal as a continuous reticulum with nuclei at its nodes, each with more or less cytoplasm, and its borders running out into a fringe of cilia.

activity is the aggregation round the nuclei of masses of granular matter, partly nutritive, partly waste, and generally the results of the chemical activities of the essential elements upon matters imported from without. Another sign is the development, in animals at least, of active movements, which involves the gradual specialisation of the filamentous elements until they become almost the most prominent factor in the organism. This explains why the filamentous connec-

tions, though universally present, remain permanently obscure in the plants, while in the animals they are gradually specialised into muscles, tendons, nerves, etc.

It will be seen, in the later chapters, that the very differences between these specialisations and the peculiarities of their distribution seem to necessitate the assumption that all plant and animal forms must have been developed out of some common continuous reticular system, continuous throughout the whole

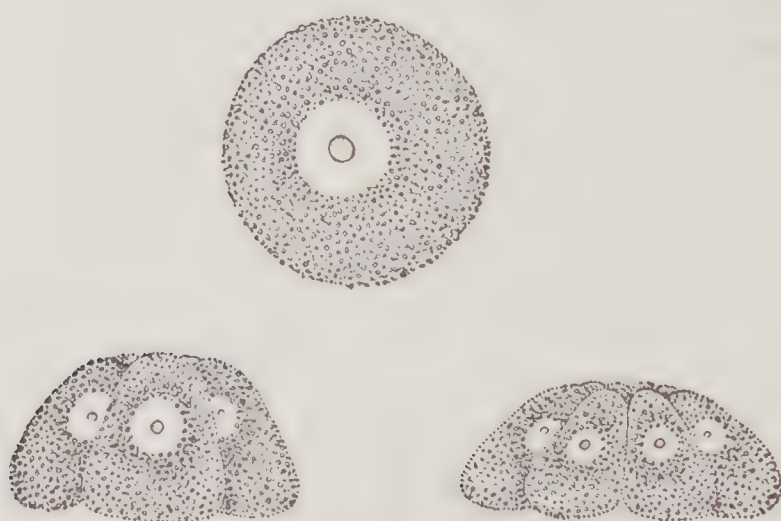


FIG. 15

Cleavage stages of *Sycandra raphanus* (after F. E. Schultze).

organism, such as that the existence of which we are now endeavouring to establish.

Having thus tried to show phylogenetically that the passage from the protoplast to the metaplast took place through the *gradual development of a continuum*, the nuclei multiplying without rupture of the filaments, let us consider the subject ontogenetically, *i.e.*, let us try to show that the passage from the egg-cell to the adult is also the gradual development of an organic continuum.

It is very important to prove this because the apparently complete cleavage of the egg is one of the

chief supports of the theory that the metaplast is originally a colony of separate individuals. Each spherical egg appears to divide up into a number of smaller distinct spherical blastomeres. Of course no rupturing of the filaments was assumed simply because no filaments were recognised as being present. But the assumption that the eggs are completely divided amounts practically to the same thing.

Now the real significance of this appearance of complete division of the egg into separate blastomeres has already been explained. It rests entirely upon the extraordinarily compact manner in which the masses of granular matter rearrange themselves round the nuclei after each division. These masses of nutritive matter are specially obtrusive at this stage because, for the needs of the growing organism, an enormous quantity has been stored up in the egg, but the linen network on which the organic unity depends, and which is at all times difficult to see, is now hopelessly obscured by the amount and density of these very accumulations.¹

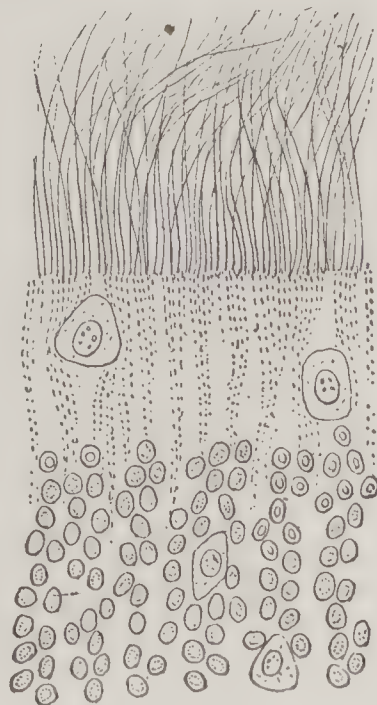


FIG. 16

Part of the edge of an embryonic Sponge (*Esperella*, after Yves Delage), magn. 750 diam. to show the cilia rooted down among the nuclei.

¹An interesting observation made by Mrs. G. F. Andrews and recorded in "The living Substance as such and as Organism," *Journ. of Morphology*, xii, 2, suppl., shows that, at times, traces of filaments may be seen in living embryos. The following is the somewhat quaint description given by Mrs. Andrews of what she saw. During the cleavage of the Echinoderm egg, the blastomeres "spin" delicate protoplasmic fila-

So perfectly divided are these "cells" supposed to be that it is sometimes said that they can be shuffled about upon one another like a pile of billiard balls and yet develop together into a perfect embryo in whatever order you leave them. This is, of course, from our standpoint, an exaggeration. The amount of possible movement upon one another must depend entirely upon how much the fundamental reticulum can be strained in one direction or another without serious derangement of the essential order of its filaments upon which the development of the organism depends. It is essential to a right understanding of our theory, however, to remember that, in all eggs that appear to divide up into "Zellenhaufen," the filaments of the network, *though invisible, are present,*

ments by which direct protoplasmic continuity is established between them subsequent to each division. From our point of view, this admits of a simple explanation: the matter "spun" by the blastomeres was supplied by the cytoplasmic matter which ran out along the connecting filaments. Hence, the filaments seen by Mrs. Andrews imply the prior existence of the still finer protoplasmic filaments which unite the nuclei into an organic whole and supply paths for cytoplasm to pass from one to the other. Without such connections in the earliest stages, the subsequent stages in the development of the embryo are incomprehensible. A comparison of Fig. 15 with Fig. 14 shows significant changes. The balls of Fig. 15 have ceased to be balls in Fig. 14 because the cytoplasmic matter has been used up. They have become stellate bodies joined by rays. When the rays of adjacent cells touch, we have cell bridges, or Mrs. Andrews's spun filaments, which means simply that the linin filaments of the reticulum are, in these cases, conveying streams of matter from one to the other. When this streaming is interrupted, perhaps by the action of the fixatives, the linin filaments disappear from view, and the cells appear as so many star-shaped masses floating freely in a hyaline fluid. The sudden appearance of the filaments as soon as the dense masses of granular matter diminish seems to necessitate the belief that the beginnings of a continuous system must have been already present in the egg, and persisted as a continuum from the egg through all stages upward and always as a continuum.

joining all the nuclei together. This statement is the *corner-stone of the whole matter*, and if this filamentous connection can be established between the nuclei, first of the cleaving egg, then of the embryo, and lastly of the tissues of the adult (points I shall attempt to prove in later chapters), the protomitomic theory, in all its essential features, is proven.

In support of the presence of the filaments in the very early stages, I would point to the fact that, when the yolk is used up by the growth of the embryo, the filaments, hitherto obscured by the former, all come to light, not only as connecting the nuclei with their cytoplasmic elements into stellate masses, but also as forming the peripheral fringe of cilia (*cf.* Fig. 14 and Fig. 16). I would also call attention to the well-known fact that, in spite of the separation of the balls of cytoplasm round the nuclei shown, say, in Fig. 15, some degree of violence is needed to shake the blastomeres apart. My explanation of this is that these balls are not free: they are mere groupings of granular refractive matter round the nuclei of a reticulum, the intervening filaments of which are so delicate as to be invisible unless, as explained elsewhere (p. 34), coated over with some substance that renders them visible.

One more argument of a different kind may be brought forward, because it hangs together with the account of yolk formation given above (p. 59). If the description of yolk-discs being built up upon the filaments round small masses of chromatin is correct, then the essential continuity of the networks of the adjacent cells of a dividing egg is established. It will be remembered that the yolk was described as a reserve substance, stored upon the filaments along which, when the material was wanted, it could once more be

conveyed to its ultimate destination. This is well illustrated by the division of the egg of *Apus* which, in one of its early stages, divides first into two and then into four (Fig. 17). These four parts acquire membrane-like walls which show them to be distinct cells in the ordinary sense. But, if we follow the history of

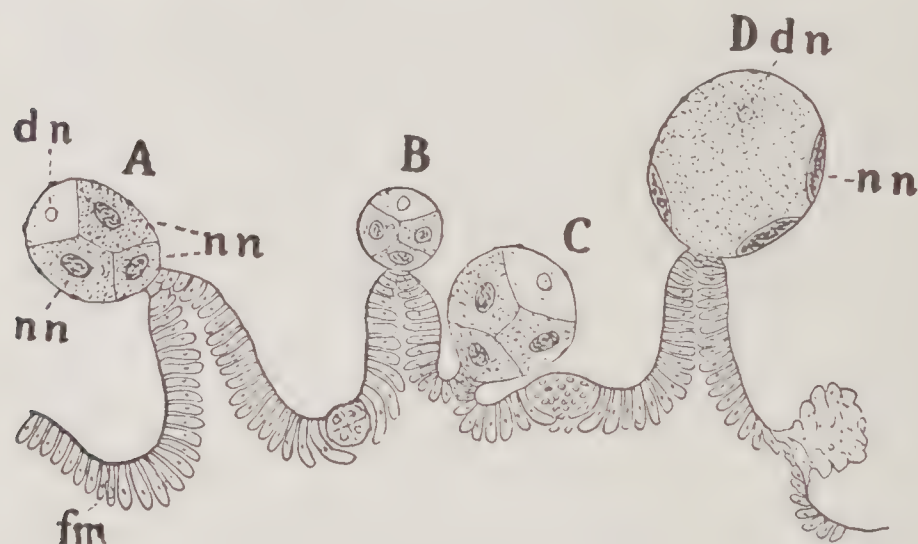


FIG. 17

Division of the egg in *Apus*. In A, B, C, an early stage of division is seen; the three nutritive cells have large nuclei (nn) while the definite egg nucleus (dn) remains small and vesicular. In D, the remains of the nutritive cells with their nuclei (nn) are seen at surface of the egg, the egg nucleus now forming the organic centre; fm, follicular epithelium.

the yolk formation as briefly given below, we find that they were at no time really distinct; that, whatever the dividing membranes mean, they certainly do not entail any real cessation of organic unity.

The nuclei in three of the cells, those furthest from the neck attaching the egg to the epithelium,¹ grow to an immense size and become specially rich in chromatin, while the fourth, the definite egg nucleus, remains small and vesicular. The three outermost cells grow

¹ See below, p. 138, for an attempt to elucidate this epithelium.

and become filled with dense masses of yolk-discs, each built, as above described, round a minute chromatin granule. As soon as this process is finished, the boundaries shift their places, and eventually move, with the nuclei which they enclose, to the side, where they remain as mere relics of the three yolk-forming cells, while the whole of the yolk is found to have the definite egg nucleus as its organic centre. Now, whatever may be the true explanation of the appearance and shifting of the membranes, and the decay of the nuclei of the three yolk-forming cells, it seems absolutely necessary, in order to obtain the final result (viz., that the yolk-discs formed on the network of the three outer cells are found on the network of the egg-cell), to assume that there were not four distinct networks but only one which ran continuously through all the four cells.

I repeat, then, that if the association between the yolk-discs and the ultimate filaments above sketched is correct (and it seems to me that it stands or falls with my principle of skeletal formation, in favour of which the strongest arguments have still to come) then this remarkable process of transference of the yolk from the yolk-forming nuclei to the egg nucleus in *Apus* amounts to a demonstration of filamentous continuity between the four apparently distinct cells in question.

It is of course true that the process just described is not exactly the cleavage of the egg, but it is the division of a "cell" into four, and if it is necessary to retain the continuity of the network for the simple purpose of arranging that the yolk shall be at the disposal of the definitive egg nucleus, it is surely more so in order to be able to ensure co-ordinated growth. Indeed, my view of the morphological and physiological import-

ance of the network, implies its continuity throughout all the stages of growth from the egg upwards as an absolute necessity.

Lastly, the essential continuity demonstrated in this way may remind us that it is not all eggs that seem to break up into so many distinct and separate cells either by the appearance of membranes or by the balling of the cytoplasm round the nuclei. Cases are known in which the nuclei can be seen to divide without the rearranging of the yolk masses so that they ball round the daughter nuclei; the yolk masses consequently remain together in a connected mass. Such cases are obviously closely comparable with the facts just described for the provisioning of the eggs of *Apus* with yolk, except that they are embryonic or post-germinal, whereas the process in *Apus* is pre-germinal, the egg being regarded as the germ. From my point of view, these cases of great masses of yolk suspended upon a continuous network in one part of which the nuclei are dividing and drawing the material for their growth and development from these yolk-discs, are of immense interest, inasmuch as they are mere variations, all equally intelligible, of the *same essential principles*: the continuity of the network throughout the organism and the synthetic functions of the filaments in relation to the yolk.

With these arguments we leave the earliest stages in the evolution of the protoplast into the metaplast, as seen either in elementary organisms or in the elementary developmental stages of more complicated forms, and pass on towards these higher forms themselves.

CHAPTER VII

THE EVOLUTION OF THE METAPLAST NETWORKS; SOME OF THE EARLIEST DIFFERENTIATIONS

IN Chapter VI we endeavoured to show both phylogenetically and ontogenetically that the transformation of the protoplast or cell into the metaplast was a process of continuous growth of the fundamental network with multiplication of the nuclei, a repetition, in fact, on a higher plane of complexity, of the earliest stage in the gradual transformation of the chromidial unit into the cell. The nuclei, in dividing and separating, pull the matters which become massed around them as centres of chromidial activity into separate and distinct masses, each nucleus receiving its share without any rupture of the network. The usual assumption that the cells are completely separate is due to too much morphological importance having been attributed to these cytoplasmic matters, which are primarily of physiological and only secondarily of morphological interest.

The simplest results of the multiplication of the cell nucleus and the extension of its network, described in Chapter VI, are large protomitomic networks of which the nuclei are the nodes. It might appear that these could grow on almost without limit as simple, uniformly extended networks, but most probably no such network ever existed, for differentiation would soon be

inevitable. Still, for the comparative study upon which we are about to enter, it will be found helpful to keep such an ideal form in our minds as the common matrix out of which all subsequent differentiations have taken place.

The forms assumed by such primitive networks are usually divided into animals and plants, but we shall

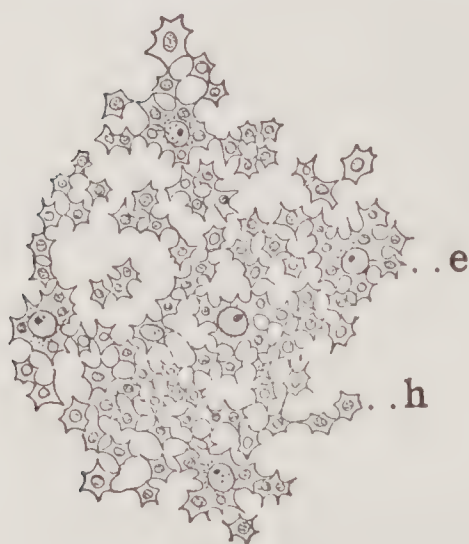


FIG. 18

Interior tissues of a Sponge (Esperella, after Yves Delage) showing the syncytium forming. The endodermic "cells" (h) are everywhere united to one another and to certain polynucleated groups (e)

for the present ignore this distinction, which is physiological, because our discussion is at first purely morphological. From this point of view it may be that these common divisions will prove to be crude and insufficient; indeed, we may question whether the early parting of the ways was confined to these two. We saw that, in the pre-cellular stage, the roots of the animal stem branched off from the original plant stem, and, as evolution advances, we may find other forms that require to be placed in lines of their

own, neither strictly plant nor strictly animal, at least unless we consent to lose all precision in our definition of these two terms.

Among the very simplest metaplasts, *i.e.*, those forms that appear to be simplest when referred back to our ideal uniformly distended network, we find the Sponges, which we have reason for regarding as morphologically and physiologically but little above

the level of the Protozoa, and which testify by their structure to the existence of the protomitomic network.

Fig. 18 shows the tissues of a young Sponge (*Esperella*) and we here find a syncytium in the course of formation. Everywhere the endodermic "cells" (h) are united by their prolongations to one another and to certain other cells.

The flagella of the Sponges may, I believe, be claimed, like those of the protoplasts, as witnesses of a continuous network of which they form the external fringe. Further, according to the well-known spongologist Ijima,¹ the trabecular network of the Hexactinellid Sponges, within which the collar-cell layer is suspended, consists of "a confused cytoplasm or nucleated protoplasm (syncytium) in the form of threads and membranes," *i.e.*, of a common protoplasmic network with scattered nuclei, but without any distinct cells; which, being translated into terms of the protomitomic theory, means that the cytoplasmic materials are distributed along the strands of the fundamental reticulum, joining together the masses of it that are aggregated round the nuclei.

In Chapter V, we saw that there is strong evidence in favour of the belief that the shells or outer coverings of the protoplasts are built up by the active agency of the protomitomic filaments. Certain materials resulting from the metabolic processes of the organism travel outward along the filaments and coat the outermost fringes of the network, together forming a compact layer. May not what is essentially the same process take place in the often gigantic protomitomic networks of some of the Sponges, in which, be it noted, we find exactly the same variations in the

¹See *Journ. Coll. Science, Imp. Univ. Tokyo*, xv, 1901, p. 160.

materials (lime salts, silica, and some chitinous or horny substance called spongin)? I would suggest that the protomitomic network helps to account for the formation, in some of the siliceous sponges, of the spicules which, when cleaned of organic matter, are found to be, as, on this assumption, they should be, hollow tubes open at both ends. Their shapes, with few exceptions, are such as might be produced by matter hardening round the threads of a network. The radiate forms of spicules, which are so numerous and so characteristic, might arise at nodes where the filaments meet. The strands of the underlying protomitomic network might, in this way, be visualised for us in silica.

The flagellated chambers of the Sponges, again, lined with their collar-cells, each with its flagellum vibrating and keeping up the streaming of the water in the chamber, seem to speak for the existence of an underlying network of filaments. The movements of the flagella and their association with nuclei have already been dealt with. The membranous collars are highly contractile and sometimes appear longitudinally striated as if by fine contractile filaments.

When we take all these mechanisms into account, it is impossible to imagine that the cells composing the sponge body were ever free and distinct cells as the original cell-colony theory demanded.

As further evidence of the fibrillar continuity of the whole organism, we may note the fact that, although there are no specialised nerve strands, a Sponge can, if stimulated, contract as a whole, like a protozoan or, shall we say, like a primitive protomitomic network, every filament of which is both nervous and contractile and not yet specialised for either function.

We pass now to another primitive metaplast net-

work,—a plant, which feeds like other plants by the assimilation of inorganic matters with the aid of chlorophyll and also by the secretion upon its filaments of the cellulose skeleton which seems to be a constant product of plant metabolism. I refer to the alga *Caulerpa* which, internally, has no separate cells, the

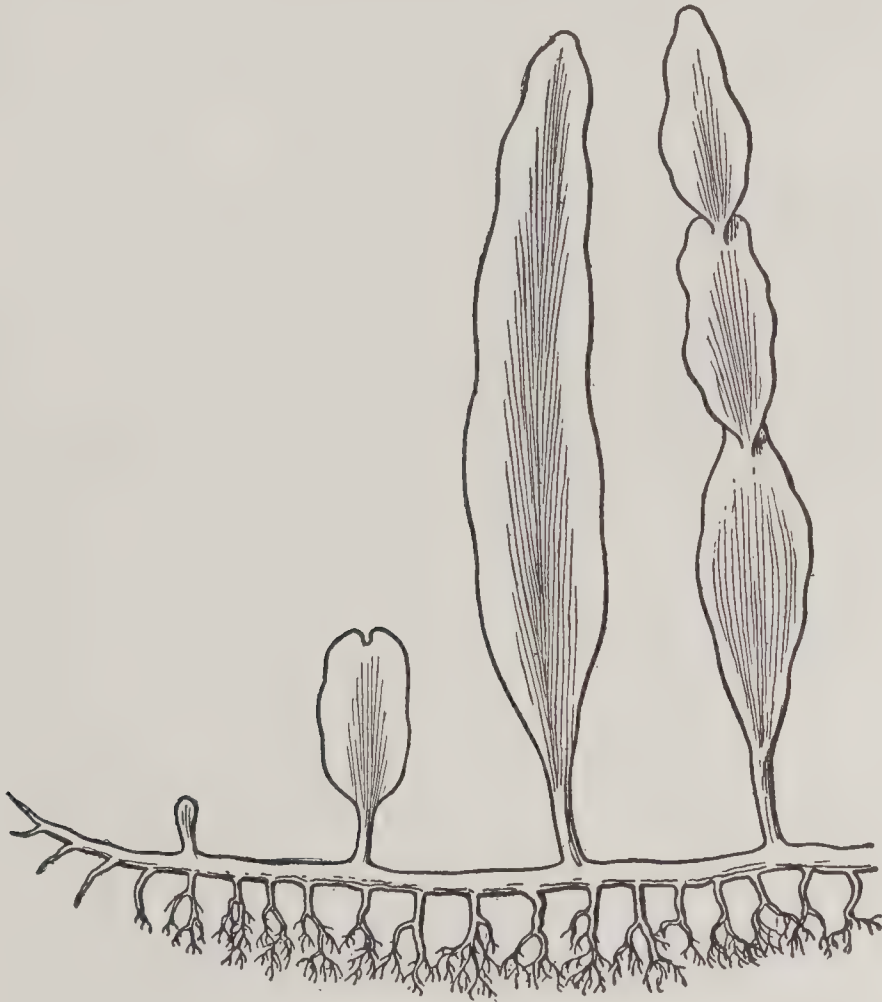


FIG. 19
Caulerpa.

protoplasm being distributed throughout the whole in reticular or nucleated strands. The supporting skeleton of this protomitomic network not only holds the plant erect but takes root in the sand or mud, sending out processes exactly like true roots, while, above ground, it is able to rise into feathered leaves and other forms closely resembling plants (Fig. 19). There is,

first of all, a complete cellulose covering which enables the plant to take definite shape and, when rooted, to stand upright. Now, not only do the cellulose walls, according to my principle of skeletal formation, bear witness to the presence of our network (see p. 68, Fig. 6), but we have here a striking illustration of a phenomenon to which frequent reference will be made further on, the travelling along the filaments of materials for skeletal formation, these materials sometimes harden-

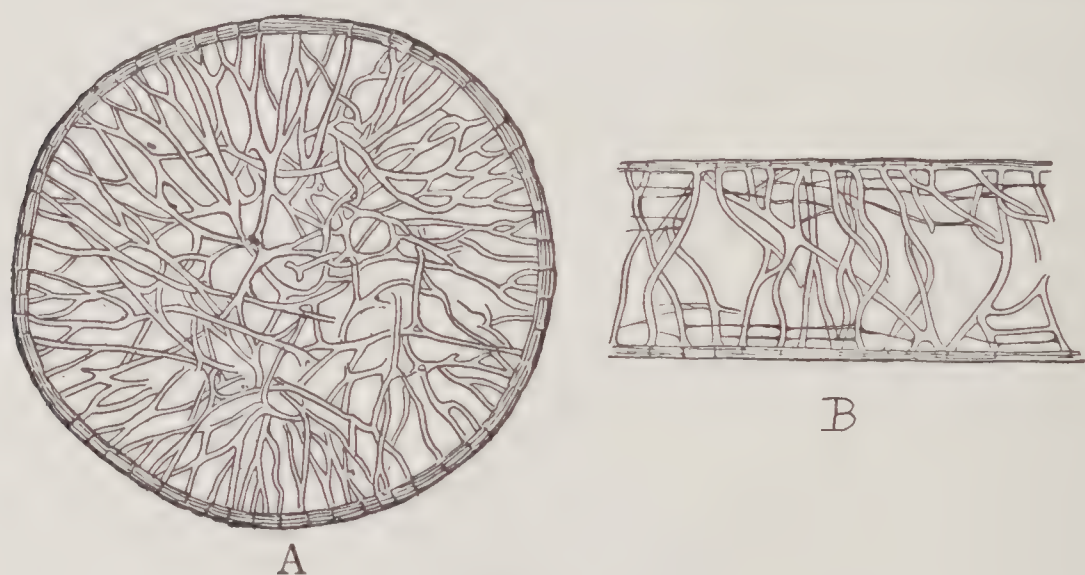


FIG. 20

Caulerpa. A, a longitudinal section through a "leaf"; B, a transverse section through the creeping shoot (diagrammatic).

ing before reaching the surface. In the case of the alga *Caulerpa*, part of the material for the cellulose walls travels along the filaments and is built up into a continuous outer covering for the whole organism, while another part actually remains upon the filaments, there hardens, and forms an internal cellulose skeleton. The forms assumed by these internal frameworks in *Caulerpa* are very suggestive. Sometimes they seem to be a more or less even network, at others they look like "so many pea-sticks stuck into the wall"¹ (Fig. 20, A

¹I am indebted for this graphic simile to my friend Prof. J. B. Farmer.

and B). The former condition bears witness to the continuity of the reticulum, the latter to the streaming of the material outward, beginning as thin streams which gradually thicken towards the surface.

The "protoplasm" itself not only lines the walls and coats these trabeculæ, but also fills all the spaces with a network of strands, as it should do according to our theory.

Caulerpa thus appears to be, in the vegetable kingdom, an almost exact analogue to the Sponges in the animal. Both of them are examples of organisms still existing which have persisted, almost undifferentiated, in adaptation to various environments. Other such forms there may be, the special morphologies of which, however, have been missed, the fashion being to try to analyse all organisms by means of the cell-colony theory. Now that we have, in our plastic network, a new instrument of research, still more such forms may be discovered. These two, the Sponges and *Caulerpa*, must, however, suffice us here, as illustrations of organisms which are little more than a protozoan and a protophyte respectively, both of gigantic proportions, yet showing hardly any advance in organic complexity.

Although the Sponges and *Caulerpa* are thus, in many ways, easy to refer to our ideal network, they deviate from the more or less round or globular shape assumed for the simplest form of network. *Caulerpa*, indeed, with its often pinnate fronds, has entirely departed from this type and the reason is not difficult to understand. Its method of obtaining food by means of chlorophyll necessitates as large a surface as possible, and the outer cellulose wall would tend to fix any growth shape assumed. The globular form is, however,

retained by other simple metaplasts, notably by the fossil Porospheridæ, the commonest form of which resembles a pea or a marble. Dr. Hinde has recently shown that these forms were very sponge-like, though their spicules were simple as compared with the marvellous developments found in the Sponges proper, and the arrangement for the outflow of the food currents was less highly specialised. In their thread-like, reticular skeletons built of fused spicules, we have the simplest of all kinds of supporting frameworks, viz., those in which the fundamental filaments themselves are stiffened almost *in situ* with hard matters.¹

The next form which we can claim with confidence as primitive and yet in advance of *Caulerpa* or of the Sponges is the alga *Volvox*. The evidence that it can also be referred to a simple network is more complete than in the case of the Sponge. This organism is, further, of special interest to us, because it not only shows an approach towards the skeletal formation which has become typical of the higher plants, but supplies us with a clear illustration of the fundamental filaments being made visible by streams of matter travelling along them.

Volvox, according to our method of analysis, is a small metaphyte network with its nuclei arranged in a special manner, viz., in a single layer round the periphery so as to leave the central region traversed by filaments alone, *i.e.*, free from nuclear nodes (Fig. 21). It is globular and moves through water by means of cilia which can be traced inwards to the protoplasmic

¹ All the higher and more elaborate skeletal systems can be shown to be but variations on this principle; they differ merely in the fact that the stiffened filaments have acquired special arrangements.

masses which envelop the nuclei. According to the old formula, these masses are the cells. For us they are merely the nuclear nodes of the network round which, as centres of chemical activity, the cytoplasmic matters are aggregated. And these centres are joined by visible strands which are, according to our view, streams of matter passing from one centre to another along the invisible filaments of the network. No fila-

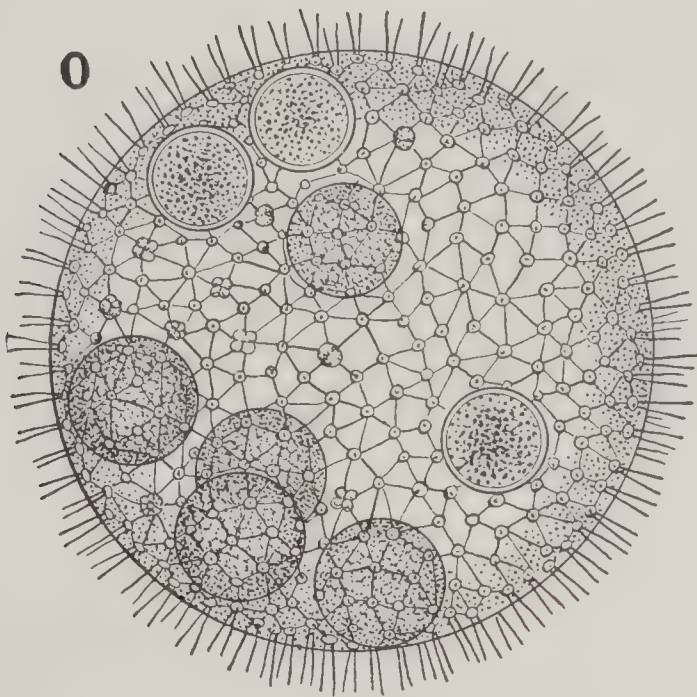


FIG. 21

Volvox aureus (from Strasburger's "*Lehrbuch der Botanik*") O, oogonium.

ments are seen crossing the central hollow, because no visible streams of matter pass across.

The skeleton supporting the whole consists, as in *Caulerpa*, of a complete outer covering of cellulose, pierced, apparently, by the cilia alone. Within this outer covering, a honeycomb arrangement of compartments projects inwards in such a way that each of the so-called cells has a compartment to itself. These compartments, closed externally by the general cover-

ing, are also closed internally by a layer of cellulose concentric with the outer covering. Each protoplasmic "cell" is thus, as in the higher plants, confined in a complete chamber or cell, in its literal primitive sense.

Now, speaking from the point of view of our theory, these chamber walls must be built up by invisible filaments radiating from the nuclei and passing through the walls, for, as explained above, p. 68, it is by and round the filaments that the walls are built. Two of the radiating filaments are visible as cilia and, as such, pass through the wall to the exterior. Other pairs are also visible because, along them, streams of matter pass; these also must pierce the walls, although their apertures, like those of the wall-building filaments, are too fine to be seen. They have to be assumed, as we also have to assume the existence of filaments traversing the sap of the central chamber; to this point we shall return. We find a reason for the streaming of materials in the ripening of eggs and sperm and the needs of the parthenogenetically produced young. A nucleus here and there grows rapidly and sinks into the hollow of the sphere where it remains suspended and fixed in place upon the filaments which, as above assumed, must traverse this sap space. We can see the filaments on that side of these germs or young organisms nearest to the layer below which they have sunk. Indeed, in sinking, they naturally brought down the filaments which, from the first, joined them to their neighbours. We see them because, again, the matter required for growth may be continually streaming along them (Fig. 22.) Now, we are certainly justified in arguing as follows: given these filaments made visible by streams, it is a mechanical necessity that they should be counteracted by others which attach the young to

the other side of the hollow, otherwise the latter could never keep its place during the movements of the whole organism as it rolls through the water. Here, then, we have conclusive evidence for the existence of filaments of the network other than those which we can see, filaments radiating from the nuclei and traversing the whole organism; those only come into sight along which streams of matter pass from one part of the organism to another.

That this is the true explanation of the visibility of these filaments is shown by the direct observations of Meyer who demonstrated, by actual experiments in treating *Volvox* with reagents, that the streams running along the filaments from nucleus to nucleus, or at least those stretching out from each

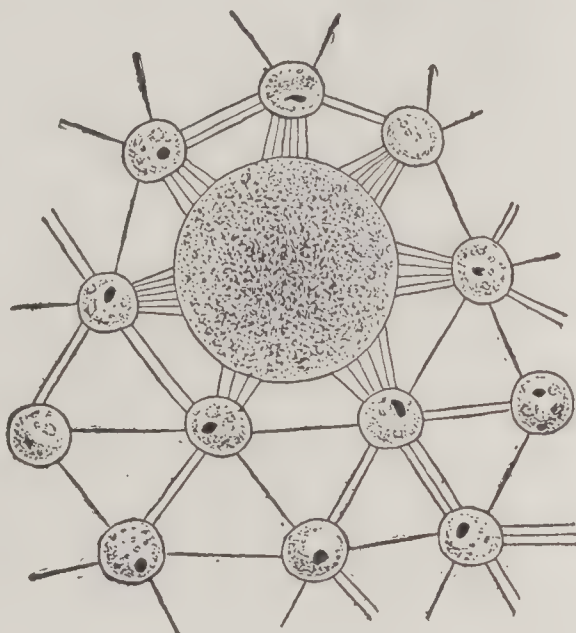


FIG. 22

An oogonium or egg of *Volvox aureus* (magnified 572 times), after Klein, from Lang's "Lehrbuch der vergleichenden Anatomie," 2d ed., with a few of the "cells" or energids. All are joined together by "cell-bridges," *i. e.*, by protomitotic filaments rendered visible by coatings of cytoplasmic matter.

nucleus to the wall (for, as a matter of fact, passage through the wall cannot be demonstrated by observation), are seriously interrupted. Most significant for us is the breaking up of the stream into beads which remain *in situ* in a row as if suspended upon some invisible filament (see Fig. 23).¹

¹Meyer, *Botanische Zeitung*, vol. 54, p. 187, pl. viii, 1896.

Meyer also found specimens which had visible connections between the cells at one time, none at another, but he suggests that this was a difference due to age. According to our view, already applied above in connection with and in explanation of other problems, the difference is one of physiological condition. The linin

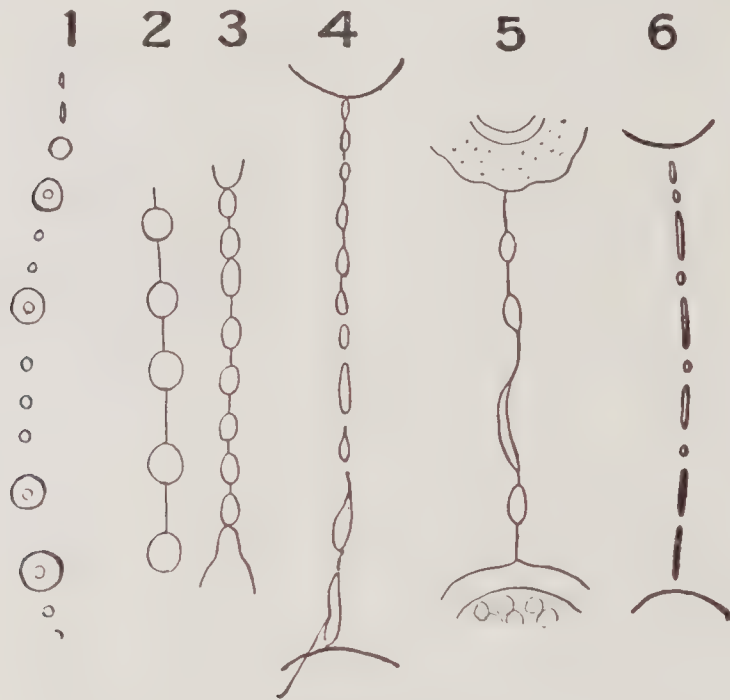


FIG. 23

Results obtained by treating *Volvox* with reagents.

1-3, after treatment with hot water; 4, after two days' saturation in acetic acid; 5, after three hours in chromic acid; 6, after treatment first with potassium iodide and next with 25% hydrochloric acid. (After Meyer.)

is in itself invisible, but may at any time become visible by streams of matter passing along it, by beads of chromatin, or by skeletal matters temporarily or permanently hardening upon it.

If this interpretation of the morphology of *Volvox* is correct, it is clear that what is seen of it under the ordinary powers of the microscope is not the real *Volvox*, but only the more visible and superficial

portions of it, viz., its surface layer of cells with cytoplasmic matters streaming from one to the other, the walls of its "cells" or chambers and its sexual products. The rest of the fundamental network, not having been seen, has been left out of account. Nor do I think that the cell-colony theory, until supplemented by the protomitomic theory, could ever have discovered it.

As a round, simple, almost evenly distributed network, *Volvox* is an excellent witness for our main contention.

In later chapters of this work, I shall have to confine myself to animal forms, but, before leaving the plants, I would like to call attention to several points of interest in their structure, as compared with that of animals.

In *Volvox* we find that chamber formation which, as a skeletal system, seems to have enabled the vegetable kingdom to clothe the surface of the planet with such vast and majestic forms. The trabecular system which depended, as in the Sponges, upon the primitive method of stiffening individual filaments or strands of filaments sufficed for small forms, but it apparently did not lend itself to any wide range of differentiation. The chamber system had all the plasticity of brickwork, if one may for a moment be false to the fundamental conception. The matter did not harden in lengths along the filaments, but in sheets across them, it being for the moment undecided whether cross filaments play any part in this formation. We have to picture to ourselves the material for wall formation carried away from the nuclei and, as it were, meeting somewhere half-way between them, and there hardening into apposed discs of cellulose. The discs resulting from the metabolism

of each nucleus unite at their edges and form a chamber round it, but a chamber perforated by the filaments which still retain their vital continuity through the walls. It is true that they are invisible but, whenever streams are passing, they may come within the range of microscopic vision in groups.¹ If the position of the chambers happens to be such that the streams are perpetual through them, the walls may become specially modified (*cf.* the well-known sieve tubes). Indeed, it is not at all necessary to follow this out, for every one acquainted with the anatomy of plants is familiar with the details; the point that interests us here is that the living part of every plant, however gigantic its proportions, is one continuous linin-chromatin network, with all the inherent properties of that network, contractile, nervous, synthetic. But whereas, in the animals, it is the first two of these functions that have been so highly specialised, in the plants, owing to their different method of obtaining food, it is the last.

Again, in *Volvox*, the cytoplasmic matter, which is comparatively small in amount, is gathered into a stellate mass round the nuclei. We are, by the way, already familiar with stellate masses in the sponge embryo and adult, and here they find again the same interpretation, the rays being due to the matter running out along connecting protomitomic filaments. In the larger plants, the cytoplasmic matters are far more plentiful and usually clothe the walls, and form what is originally known as the "primordial utricle." How far this indicates any further complication of the filaments of the network radiating from the nuclei, I do not know; what I wish specially to call attention

¹ *Cf.* the so-called "intercellular bridges" from the cell-colony point of view; see for example Gardiner, *Trans. Roy. Society*, 1901, p. 83.

to is the fact that, in plants which lend themselves to a microscopic study of the network in its living state, the cytoplasmic matter can be actually seen actively streaming round the walls and across from wall to wall, as I should say, along the filaments. Indeed, I would suggest that such movements of matter may be universal throughout the whole of plant life and that, whatever later and accessory circulatory systems may be developed in plants, or, for the matter of that, in animals also, the primitive and essential circulation is that of materials along the filaments of the network. The conveyance of these streams is, in fact, what is meant by their synthetic functions. This is, indeed, all we can say, for here we run against the great blank wall of ignorance which we meet with sooner or later turn which way we will. We do not know how the filaments convey the matter, nor why they take this in this direction nor that in that; why this matter stops here and hardens while that is redissolved and removed, nor that other cast out. The results seem reasonable enough, but the secret forces completely elude our search.

Lastly, let me point out what will hardly have escaped the reader, that this reference of all plants to our ideal linin-chromatin network will account for all those traces of nerve impulses known, however rarely, to pass through plants or parts of plants and which, when not shown by actual movements, have yet to be assumed to explain the obviously correlated growth of different parts. The assertion that the plants are not nervous organisms can only be rightly appreciated when we have studied, as we shall presently have to do, the extraordinary specialisation of the nervous functions in the higher animals. We shall then be able to

understand that the plants, while not nervous, yet have the same primitive nerve elements as the animals, and still exercise the same elementary functions of those elements, but no case appears to be known in which a plant has been specialised in this way sufficiently to lead to structural differentiation.

CHAPTER VIII

THE EVOLUTION OF THE METAPLAST NETWORKS; SOME CAUSES OF DIFFERENTIATION

BEFORE passing from organisms that show little or no internal differentiation beyond the formation of skeletal supports to those in which the nuclei and filaments of the originally homogeneous network become rearranged into sheets, bands, and strands, that is, into tissues, some of the causes of the differentiations that take place in the metaplast networks should be mentioned.

The various methods of feeding adopted by these networks may, I think, be regarded as one of the chief causes of differentiation, helping to account for all the various shapes of the organisms and their tissues. Since all growth depends upon the intake of food, it is evident that the large multi-nucleate networks, in order to attain their size, must have acquired some efficient method of obtaining large supplies of nourishment. The two processes of feeding and growth go hand in hand. I would draw attention specially to three methods of feeding, all distinct from one another and probably of independent origin.

A method early developed in animals consisted in the formation, by the network, of a large central pocket into which other organisms or parts of organisms find their way and in which they are dissolved, the juices thus

obtained being absorbed by the network. This method must have resulted from some primitive gullet-formation, the gullet enlarging as a gullet, *i.e.*, as a single large pocket, and not as in the Sponges, where the gullets multiplied, grew inward, opened into each other, and formed a canal system ramifying throughout the body.

Other networks, instead of drawing in organic matters and dissolving them inside, spread themselves out over the surface of the dead or unprotected bodies of other organisms, dissolving them and, in that way, absorbing them. This method would soon involve the sending down of long threads into the interior of the mass, to penetrate to all parts until the whole was dissolved and all that was nutritive absorbed. This is the method typical of the Fungi, and may have been adopted more than once. There is no reason why the earlier chromidial networks may not have thriven on this method, and survivors of such networks, larger than the Microbes, whose manner of life is essentially the same, may still persist side by side, perhaps, with metaplastic networks such as the Myxomycetes, which certainly live in this way and may be the analogue or one of the analogues of the Fungi on the higher plane of the metaplast.

The earliest method of feeding, however, is probably that of the plant networks. These built themselves up out of materials which, for all we know, were never previously combined to form organisms. They grew by a process of adding material from the air, water, and earth.

I have called this the earliest method, for it is probably along the lines indicated by the feeding of plants that the physiological chemists must grope after the beginnings of life. I would suggest that the plants are

the direct descendants of the very first organisms that arose out of an entirely inorganic medium. Once an organism was started and some extremely simple unit of organic life appeared, probably prior to the chromidial unit that has here been tentatively postulated as the first that we can at present recognise, the ball would be set rolling and would gather velocity as it went. These first organisms would supply ready-made material as the food of other organisms and the Fungi and animals, the results of other methods of growth, would be added to the plants, the plants themselves taking a new and higher flight by the aid of the material supplied by their dead comrades.

Of these three methods of feeding, that of the plant, of the animal, and of the saprophyte, the last is the one that would call forth least differentiation on the part of the feeding organism. Hence the Fungi, built of the simple, hyphal tubes, have remained a tribe by themselves, and continue at a comparatively low level of complexity. The plants I would suggest come next in order in this respect. They develop, out of the elements, special chlorophyll organs that must have been present in the very first molecular complex which was the foundation of all organic life, and not only present, but functional as chlorophyll, though in a very rudimentary manner. With specialised chlorophyll organs and with dead organisms supplying ready-made material, the power of growth of the plants was so enormous that they were able to people the whole world and to invade so vast a range of environments that their names and variations are legion. Their complexity, however, remains simple as compared with that of animals. They live, but some of the elementary functions of the linin and chromatin network, developed

as essential to all animal life, remain in the plants even to-day practically stationary at their primitive condition, and this causes the enormous gulf that yawns between life in Man and life in the tree under whose shade he rests and whose skeleton he uses in a thousand ways for the enriching of his own life. It is the animal, with his food-pocket and the necessity to fill it, that has carried life, in the widest sense, to ever higher levels of organic complexity.

We have seen that the two processes of growth and feeding have gone hand in hand, but, indeed, all the essential processes must have gone hand in hand. Increased size means not only increased food supply with increased efficiency of excretion, but also more efficient skeletal support. These differentiations must go on concurrently if any high degree of complexity is to be reached. And, further, the lines of development of these early differentiations must be such that they can mutually aid each other if there is to be any evolutionary advance; the whole complex of the organism has to remain plastic so as to be adaptable in the event of changes being required in any of its parts. This seems to be a prime necessity if any high degree of development is to be attained. Mutual adaptability between the parts of the complex is not enough, but mutual adaptability has to be retained, otherwise plasticity for continued advance is lost.

The Sponges supply us with a good illustration of the absence of such adaptability, leading to a deadlock. We find, in them, an interlacing skeleton most perfectly adapted to their special canal system of feeding, but the organism necessarily remained too rigid for further development. There was perfect response to a very elementary and uniform environment, but the internal

machinery by which success was attained was of a type that would stand in the way of any fundamental rearrangement of the internal parts. Other networks, not hampered by such a skeleton, have therefore pushed past the Sponges. If, here and there, descendants of the Sponges may have tried to rise above their own low level of perfection, they have apparently not succeeded, but have been left behind in the race.

We must also bear in mind that these living networks, at every stage of their differentiation, are subject to the interaction of two kinds of forces, internal and external. The internal forces may be summed up as the power the organism possesses of assimilating material, either adding it to its bulk so as to grow, or using it for the production of energy so as to be able actively to respond to the attractive or repellent impacts of the environment, while the external forces are the sum of these impacts of the environment. The progress of life and the fundamental principle of evolution are to be found in this interaction. In this chapter we have to deal only with some of the very simplest responses.

In illustration of the gradual differentiation brought about in the early metaplasts, and as a transition form between the ideal uniform network and the animals with distinct tissues and organ formation, I shall here briefly sketch the morphology of the Coelenterates.

We may again start with a network of rounded form, but one no longer taking in its food as small particles washed into channels in the network by currents of water, as in the Sponges. The surface of this organism appears to have yielded before and perhaps folded round organic masses which came into contact with it. Whatever the exact mechanism of

the process, the result was that food masses found their way into a central cavity of the network—a cavity which became lined with a compact layer of nuclear nodes forming a digestive epithelium. A central digestive organ would in this way originate as an efficient method for the nourishment of the body and the supply of vital energy. Its efficiency, indeed, is proved by the fact that, in the race for life among animals, the “stomached” forms have triumphed.

In this early Coelenterate, we find the three primitive layers of epithelia of current morphology: the ectoderm, the layer of nuclei at the outer surface, the endoderm, lining the digestive cavity, and the mesoderm, the remains of the original network between the digestive pocket and the outer covering. Given our ideal network, these “germ layers,” which have led to so much controversy and theorising, are reached in the simplest and most natural manner possible.

Another important differentiation took place at about this stage. The coelenterate network was not necessarily small and would, in almost any case, require support, if only from the fact that it contained a large cavity inside. This question of support has, as we have seen, been a fateful one in the evolution of life, Protozoa having become stationary through the ages owing to the perfection of their skeletal frameworks and Sponges having been so hampered as to be unable to reach any high level of organic differentiation. In view of this, a brief mention of the various methods of protection and support adopted by these stomached networks is not only instructive but of great importance for our general argument, for it would be difficult to co-ordinate the various coelenterate skeletons more simply

and easily than we are able to do by means of our fundamental network.

The primitive method of the Sponges was adopted by some of the early Coelenterates, the filaments of the network surrounding the digestive pocket and passing from it to the ectoderm becoming coated with hard matters. The organism was thus supported by a mass of spicules. The descendants of such forms, the Alcyonarian Corals, show great variety and beauty of structure but have remained stationary at their low level of development, for such a skeletal method is almost prohibitive of any high development of organic formation.

Other early Coelenterates, the primitive Hydrozoa, adopted a method of support full of possibilities of future development. The digestive cavity increased in size to the utmost, squeezing the whole of the network situated between the pocket and the ectoderm into a thin lamina, the matted filaments of which, while becoming coated with elastic matter, or specialised for muscular contractions, or as nerves, formed at the same time a plastic and adjustable support and powerful walls for the digestive sac, allowing of great distention for the reception of large quantities of food. Such an organism thus acquired two qualities of supreme value in the race for life: immense powers of assimilation and great capacity of vigorous response to the impacts of the environment. One group of these organisms, however, developed a skeletal covering into which the soft body could retreat and gave rise to the stony Corals which, again, like the Alcyonarians, though showing marvellous variation in the details of their skeletal arrangements, have never been able to rise to any higher level. They acquired stability at the cost of progress.

The primitive Alcyonarians, as I said, produced hard skeletons by the accumulation of hard compact masses of single spicules upon the filaments of the network which persisted between the endoderm and the ectoderm. In the Corals, this network was no longer available for such a purpose; it was already squeezed into a lamina of fibres more or less highly specialised for other functions. The skeletal matter could therefore harden only upon the filaments outside this specialised lamina, that is, those running outward through the ectoderm and forming the outermost fringe of the whole network. We accordingly find that the skeletal parts of the Coral are formed by the coating of those filaments which, in the larval state projected as cilia. The matter passing out along these soon turns them into a compact and solid layer of prisms. In this way the basal half of the coral polyp builds up the stony cup into which the upper half can retreat by contraction. If the walls of the polyp are folded, as in the formation of a septum, the hard matter is discharged from both sides of the fold and the tips of the prisms have to meet in the middle line. Here one might expect them to interlock, and in some measure doubtless they do, but other organic matters travel outward along the filaments and, accumulating, form the middle dark layer characteristic of the septum of the coral skeleton, at one time called, by puzzled morphologists, the "primordial septum."

It is important to notice that the essential principle in these two kinds of skeletal formations found in Coelenterates is the same in both cases. Both are due to the coating of filaments (in the one case of filaments within the body, in the other of filaments projecting from the body) with hard matters.

Any one at all acquainted with the many attempts that have been made to solve the problems of the coral skeleton will welcome this simple solution, supplied by our analytical method of referring the organism to a linin-chromatin network. The very fact that it enables us to explain the apparently entirely different skeletons of the Madreporaria and the Alcyonaria as simple variations of one and the same essential vital principle appears to me a strong argument in its favor.

This description of the morphology of the Cœlenterates differs widely from that supplied by the cell-colony theory. According to that doctrine, the ectoderm and the endoderm were originally the only cell constituents in the cœlenterate body, each of them being a single layer of "cells" which had come to be so arranged through the invagination of one half of a hollow sphere of cells into the other half, the result being the famous Gastrula of Prof. Haeckel's *Gastræa* theory. The layers of cells, it is said, secrete a gelatinous lamina between them. This was supposed to be the primitive condition, and all other conditions, *e.g.*, that in which this lamina contains a multitude of fibrils and is even thickened so as to require skeletal supports, as in the Alcyonaria, are supposed to be secondary, the "cells" seen in it having migrated, mostly from the ectoderm. The first appearance of the fibrils is said to be due to the sending out of "neuro-muscular processes" from certain of the cells of the ectoderm, which then gradually sink below the surface to become muscles and nerves.

In these rival accounts of the essential morphology of the primitive Cœlenterate, we have an excellent illustration of the difference between the protomitomic theory and the cell theory of the metaplasts, and there could be no better object in connection with which

the superiority of the former could be demonstrated. The invagination of a hollow sphere of blastomeres in that much discussed ontogenetic phase known as the gastrula, and the recognition by Haeckel of the possibility that this gastrula might represent the coelenterate stage in the development of animal forms, came as the first concrete instance of the mechanics of evolution according to the cell doctrine. It was convincing, because it was so fundamental. And it cannot be doubted that both the cell doctrine, the doctrine of evolution, and the law of biogenesis received immense support from it. That it comes near the truth there can be no doubt. But it presents some insuperable difficulties, which are avoided by the protomitomic theory; the latter also explains the facts with even greater ease.

Among these difficulties, which can be avoided by the acceptance of the new and more comprehensive theory, we find the following.

I. There is no special reason why the sphere of equal and separate blastomeres should invaginate for the purpose of feeding. But if there is a spherical network, already organised, which acts as a whole, and feeds by folding round food particles with which it comes into contact, we have a *causa efficiens* of the bulging in of the outer layer.

II. The Gastræa theory, according to the cell doctrine, assumes that the extreme forms, that is, those with the largest cavity and the thinnest, most specialised walls, are the primitive forms; the rise of the so-called mesoderm is accounted for secondarily. This is surely most improbable; extreme forms are seldom primitive. Apart from any special theory of its origin, the smaller cavity, the more undifferentiated

walls, either simply parenchymatous or filled with spicules, are far more likely to be primitive than the highly contractile walls of the Hydra. Recent research has thrown some light on the real nature of the tissue between the ectoderm and endoderm in the Alcyonaria, showing that in the typical Alcyonarian, in which the middle layer is still conspicuous, its primitive reticular character is still traceable. Miss Anne Pratt¹ has not only seen this, but has also seen the cytoplasmic matter round the nuclei of this reticulum showing amœboid movements. She noted, further, that stained food particles could travel along the filaments, for instance, from the endodermal "cells" which ingested them to the ectodermal. Miss Pratt points out therefore that this reticulum, which has always hitherto been regarded as exclusively nervous, is not so. It is, in fact, the undifferentiated protomitotic network, the filaments of which are capable of performing all the primitive vital functions.

Where the layer between the ectoderm and the endoderm is thickest, therefore, its condition is most primitive, as we have already gathered from the primitive character of its skeletal formation. But where the layer is thinnest, as in the Hydra, the Sea Anemones, and the stony Corals, the structure of its walls as compared with those of the Alcyonarians is most instructive. Take the Hydra, which has been much studied. The ectoderm lends no support whatever to the idea that

¹ *Zool. Anzeiger*, 1902, p. 545. See also the fuller paper, *Quart. Jour. Microsc. Soc.*, 1905, p. 327. In this Miss Pratt calls attention to the fact that the stellate cells seen in fixed preparations are, in reality, due to the retractions of pseudopodia which primitively formed a continuous plexus. But this continuous plexus of protoplasmic pseudopodia is explicable if there are fixed filamentous paths along which the protoplasm stream.

it was ever composed of a single row of blastomeres secondarily squeezed into what is called a columnar epithelium. Many students who, guided by the gastræa theory, expected to find such an epithelium have been strangely puzzled to find, instead, a very irregular, compact layer of cells of all sizes and shapes jammed together two or three deep, just such as might be produced by the nuclei of a network having been massed together at the surface by the squeezing of the network itself into a thin layer. Some of these energids can be teased out and are then found connected with fibrils which run into the mesoglæa, as we should expect. They are not "neuromuscular epithelial cells" but merely portions of the neuromuscular reticular linin-chromatin system teased out after having been compressed together into a lamina. Indeed, the very formation of the elastic gelatinous substance may be referred to our principle of skeletal formation. We must claim it as produced by the coating of a proportion of the filaments of this condensed network with materials which could produce the result. In other words, the feltwork of filaments was there before the elastic lamina.

III. We have also the difficulty of correlation,—that insuperable difficulty against which, as against a wall, the cell doctrine has always struck. There is no *reason* why the ectoderm cells of the gastrula should put out the neuromuscular processes which have then to seek their points of attachment, the processes being useless until these points are reached.

Merely to point out that our view of the Cœlenterate as a continuous, multinucleate network is in harmony with all these facts that are inexplicable by the cell theory is, however, not all that we can do. We have

positive evidence to adduce. We can point to the cilia of the coelenterate larva, which are known to belong to the fringe of an underlying reticulum; to the marvellous contractility of the typical Coelenterate and to the fact that the contraction is always harmonious and perfectly co-ordinated, any part being able to contract or expand by itself, or all parts together;—we can point to all these as witnesses that the contractile tissue, *i.e.*, the whole body wall, is, and always was, a continuum.

We also have evidence from the skeleton. In the Alcyonaria, which have kept the thick middle layer, the spicules occur in this layer, but when this layer is squeezed into a thin lamella, there is no room for internal spicules. The hard material which may be safely regarded, in part at least, as metabolic waste has, in the stony Corals at any rate, to be carried, by the filaments, outside of the body. This certainly argues an organic continuity between the coated filaments and the interior of the body. Here and there, indeed, bundles of filaments can be seen running into the skeleton because, in some way or other, modified so as to act as the attached ends of other filaments specialised for contraction. In such cases, we find filaments buried in the skeleton like the ordinary skeleton-forming filaments, but stretching great distances through the body as muscle fibres.

The nematocysts have already been alluded to as only intelligible as products of an organism the texture of which is essentially filamentous. The trichocysts of the protoplast might be simple filaments or sheaths of waste matter deposited by the filaments, but the nematocysts of the metaplast, judging from their size and complexity, are certainly strands of filaments or

materials built up of such strands. Some are small and shot out by hundreds at a time from knob-like batteries at the surface; others are immense coiled-up springs (giant nematocysts) in close sacs inside the body and probably only released when the animal is bitten into. And between these two there are many grades. All these stings are frequently figured as if they had some kind of filamentous pattern upon them besides the barbing, and this, again, is what we should expect if the origin here attributed to them is correct.

These facts and arguments, taken all together, seem to me fully to justify us in regarding the Cœlenterates as direct modifications of a multinucleate network.

CHAPTER IX

SOME PRINCIPLES OF TISSUE AND ORGAN FORMATION AND THE SPECIALISED TISSUES THAT BIND THE ORGANS INTO A WHOLE

WE have now to try to unravel the meaning of some of the internal differentiations of the metaplast network which led, through tissue formation, to the formation of specific organs. The complication of the organism is progressive: the tissues, being the formative material out of which the organs are built, come first, then, just as the nuclei and strands of the primitive network become re-arranged to form tissues, so do the tissues combine to form organs.

The brief review of some of the early Metazoa, given in the last two chapters, brought to light several important facts and principles with regard to tissue and organ formation. It became evident, in the first place, that some kind of skeletal framework was necessary to give an organism sufficient rigidity to allow of the development of any efficient organs. We saw, also, that the peculiar spicular skeleton characteristic of the Sponges and the Alcyonaria stood in the way of any but the most simple organ formation and that, consequently, forms hampered by such skeletons remained stationary at a low level of life. This *close interrelationship between skeletal frameworks and organ formation* may be claimed as our *first principle*.

We saw also that while, in such an organism as the Sponge, the function of digestion necessarily remained diffused, other forms, unhampered by a spicular skeleton, developed a special cavity for the reception and digestion of food particles, and the fate of these organisms is so different from that of the Sponges that we may lay it down as our *second principle* that *a specialised digestive centre, by relieving the rest of the organism of the function of digestion, sets it free for other purposes*. A digestive cavity may thus be regarded as the real starting point in the transformation of the undifferentiated organism into a complex of separate organs.

In the "stomached" forms so far considered, the digestive cavity opened as a cavity in a continuous three-dimensional network and was lined by nuclear nodes of this network, each having a larger or smaller amount of cytoplasmic matter around it and all together forming a layer or epithelium. Our *third and fourth principles* consequently are that *organs arise as spaces in a continuous reticular matrix and that they are lined by rearrangements of the energids belonging to that matrix*. It is necessary to emphasise these two last very obvious points, not only because the current teaching of the cell-colony theory accounts for all structural development by a marshalling of so many separate cells, but because the review of the morphology and texture of organs and tissues which is to be given in subsequent chapters refers them all to so many differentiations of a continuous reticular groundwork. Ontogenetically, the appearances certainly do suggest the marshalling of "cells," as we have already seen in the account of the cleavage of the egg and the early embryonic stage. But these appearances are quite as explicable and much more intelligible if the cell move-

ments are referred to the dividing and redividing of the yolk as it follows the multiplication of the nuclear nodes of a continuous organic network.

Our *fifth* (and last) *principle* follows directly on the fourth. It is that *these rearrangements of the nuclear nodes so as to form the layers known as epithelia are the essential structural factors in organ formation*. It seems to me that we have, in this process, a continuation, on a higher plane, of the same line of development that first gave rise to the nucleus, the principle throughout being at the same time a differentiation and a concentration of functional energies for the most efficient responses to the attractive and repellent stimuli of the environment. In the formation of the nucleus, the chromidial centres gathered into groups, and these again into larger groups, and, at each stage, the filaments of the original simple, uniformly distributed network became still further complicated, until the nucleus appeared with the strands of the network arranged round it as a centre. In the cell period, it was the turn of the nucleus to multiply, just as the original chromidium of the hypothetical chromidial unit multiplied, by what is known as doubling division, *i.e.*, always into twos. Nuclei, thus formed, again gathered into groups of various kinds, these groups becoming, through the formation of epithelia, the organs of the higher organisms. In the light of these fundamental principles, organ formation may be briefly defined as a progressive dividing up of the originally diffused network into so many portions, the energids of each of which arrange themselves so as to form organs for the concentration of the special functions. During this process, far-reaching rearrangements of the elements of the network lead to many stretch-

ings and twistings and groupings, not only of bundles of elementary filaments, as was the case when the groups of chromidia formed themselves into still larger groups, but of great strands of the network itself, *i.e.*, of those residual portions of the network left over and above that already used up for the organs. These strands and sheets of the network, with their involved nuclei, then, as the "connective tissues," take on the special function of binding the organs together as a whole.¹

That the groupings of the nuclei are the chief structural factor in organ formation may, I think, be gathered from the process of development. The very first attempt of the developing organism seems to be to produce an ectoderm, then an endoderm, and then the elements for the formation of the organs lying between the two. According to the terminology of the supporters of the cell theory, these layers are arrangements of "cells"; according to the protomitomic theory, they are merely the divisions of nuclear nodes of a reticulum round which the yolk and other cytoplasmic masses regroup themselves. Apart from this difference in fundamental conception, the conclusions drawn from the appearances by the two theories do not seriously disagree, so far as the production of the two primary epithelia are concerned, but, as already shown there is an essential difference of view with regard to the mesoderm. We shall see later that the ontogenetic appearances that have proved so misleading are not universal,—that cases are common in which the nuclei actually divide in a continuous matrix, the cytoplasmic matter aggregating around them and causing the appearance of "cells" only after they have taken their places.

¹ See pp. 140-142.

The rearrangement of the nuclei and of the strands of the primitive network in order to form tissues is accompanied by a specialisation of functions which deserves attention. The nuclei lining cavities for different purposes would attract around them the cytoplasmic matters adapted to those special purposes. Hence we find different characters of "cells" round different cavities and at different surfaces. Similarly, though primitively every filament was both contractile and nervous and capable of conducting materials for synthetic and metabolic purposes, the rearrangements of the filaments in the metaplastic network are always in the interest of special functions.

How this specialisation of function of the filaments takes place is difficult to understand. It may be by some regulation of the material substances in which they are embedded; some substances may tend to favor, others to inhibit contractility or nerve energy. It is possible that the strands which are to act as muscles may be embedded in supplies of the materials used up in the energy of contraction and thus be protected from those that would stimulate the bundles to nervous activity, and vice versa in the case of those required to be nerves. It is quite certain that these tissues show considerable histological differences, whereas, according to the hypothesis, the ultimate elements were, at one time, indistinguishable and, indeed, may be so now, if we could isolate them. It is important to note that though the network is thus rearranged to produce specialised muscles and nerves, in no case, apparently, are the other primitive functions of the filaments wholly lost. Most tissues, however specialised, retain the power of growth and regeneration and perhaps all the other inherent functions of protomitomic filaments.

These problems of the specialisation of functions will be further discussed in connection with the nerves and the sensory organs and the conveyance of materials from place to place.

Let us now try to illustrate and prove the principles of organ formation suggested in this chapter by examining some of the tissues and organs of the metaplasts more in detail.

The first step in tissue formation necessarily involves the grouping of the nuclei into sheets and rows with corresponding differentiation of the filaments. In the formation of sheets for the lining of cavities it is usually the metabolic activities of the energids that are being concentrated, hence we find the nuclei of such sheets, or epithelia as they are called, surrounded with granular matters. In the case of strands, it is mostly the contractile or nervous functions of the filaments which are specialised.

The epithelia arise as linings round pockets or cavities in the network into which matters from without are received, or else secretions or excretions from the network are collected. In either case we see why the nuclei of these epithelia are surrounded by cytoplasmic materials, since it is their chemical energies that are required to act upon the material taken in or to produce the matter discharged. In the case of the strands, the filaments only require the material necessary to permit of their contracting or of conveying nerve stimuli.

An early stage in the formation of epithelia is seen in the rearrangement of the nuclei round the flagellated chamber of the Sponge, *i.e.*, round the only approach to an organ to be found in those forms, the structure of

which is most significant. Fig. 24 shows the process of the gradual rearrangement of the cells round a cavity. The arrangement is quite loose, just as if the cavity had appeared and had been lined merely by those cells that

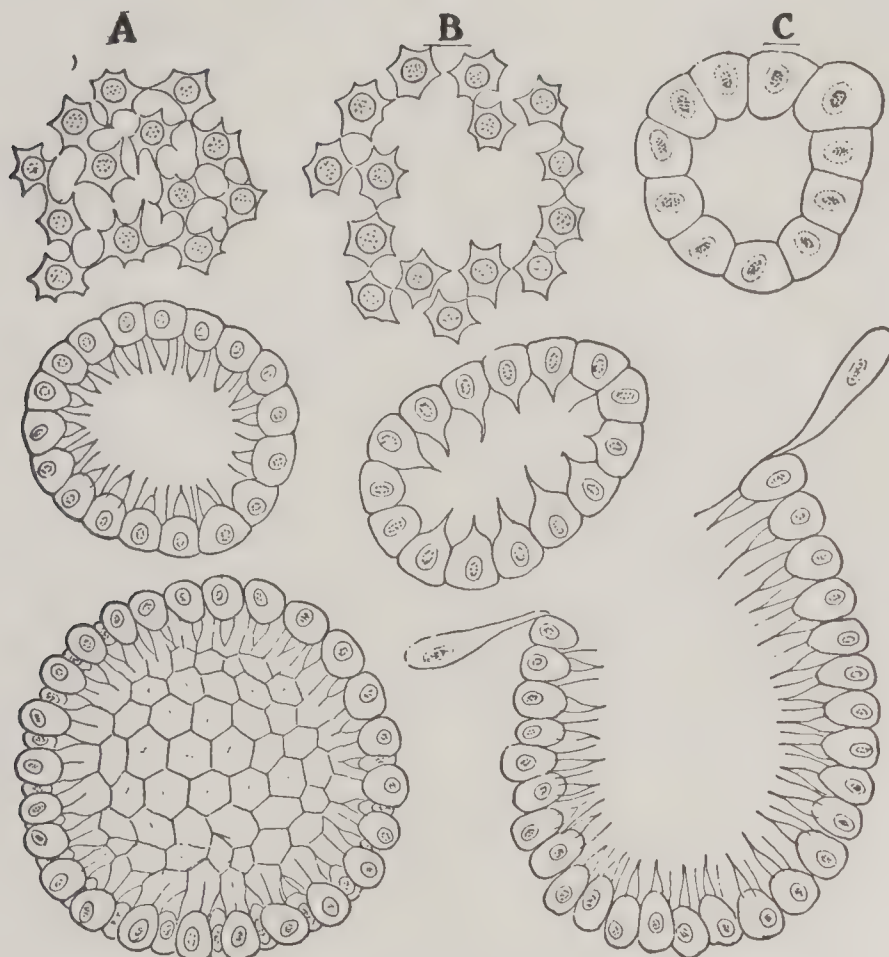


FIG. 24

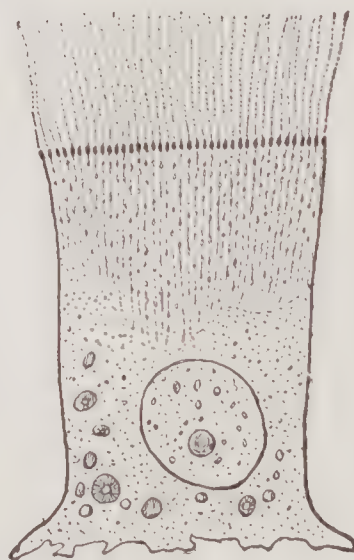
Development of a flagellate chamber in a Sponge (*Esperella*, after Yves Delage). **A.** The primitive reticulum, with the stellate nodes; in **B**, these begin to separate and arrange themselves round a cavity each of the individual energids being provided with a flagellum and a collar.

were *in situ*. The layer stops short of being made compact by the crowding in of adjacent nuclei so as to form an epithelium, because there is here no need for it to function specially as a surface, for the flagellated chambers do not receive any injected or secreted matters needing specialised walls to contain or deal with them,

but merely streams of water which can be shut off at will.¹ I am inclined to regard this as a most instructive



A



B

FIG. 25

Ciliated energids from the intestinal epithelium; A, of *Anodonta*; B, of *Cyclas*, showing the filaments running to the cilia and beaded with staining matter (chromatin). (After Engelmann.)

illustration, almost accidentally preserved for us, of the earlier primitive phases of epithelium formation. I say almost accidentally, for it is difficult to imagine how such a stage in the formation of an epithelium, which is of little use until it is efficient, could be preserved.

Such a primitive ectoderm as that of the embryo Sponge (Fig. 14, p. 91) can be referred without difficulty to the migration of the energids to the surface, where they form a compact row, because each energid can be seen running continuously inward and thus remaining united with the organism. These energids can be explained simply enough as the outermost layer of the nuclear nodes. Outside

them would naturally be found the peripheral fringe of the filaments of the fundamental network. That

¹The structure of the flagellated chambers is specially instructive when compared with that of the pockets developed for the intake of food particles by forms not hampered with a skeleton like that of the Sponges. These pockets arise by the ingrowth of that external epithelium which we find in the young Sponge during its locomotory stage when it requires cilia to propel it.

they should be seen as a compact row of cells is also intelligible, for the outermost energids would be those engaged in most active functioning.¹ They are in contact with the oxygenating medium; they require a specially large food supply for the working of the cilia, and it is round the periphery that growth must be taking place (Fig. 25).

Again it is not difficult to see why these ectodermal energids so often appear to persist as separate columnar protrusions from the surface. In view of the great delicacy of the fundamental filaments and the ease with which they are ruptured it is, of course, doubtful whether these energids ever are really separate. There is no reason to suppose that they should be, for all the lines of nervous, contractile, and synthetic energy should run radially outward, *i.e.*, along the energid, and not laterally into the energids adjoining it. Still the question may be left open. The appearance of separation is due, as in the case of the component "cells" of tissues, to the fact that the cytoplasmic matters are strongly attracted round nuclear centres and this would be the case whether the network were continuous through the lateral surfaces of the energids of columnar epithelia or not.

But all epithelia are not so simple as this; cases occur in which a sheet of energids arranged fairly compactly side by side rise up from a thin hyaline membrane; see, for example, that of the genital gland of *Apus*, Fig. 17, p. 96. Such tissues are among the pillars of the cell-colony

¹ Such compact layers of nuclei, each provided with an unusually large amount of cytoplasmic matter (witnessing to the nuclear activity of the cell), will be found later on to play an immense part in the building up of organs within our ideal network; it is this process, indeed, which obliterates any resemblance between the more complex organisms and the fundamental network.

theory, for here we have a row of apparently independent cells, independent except that they are sessile upon a common "basement membrane." How can the protomitotic theory account for such a tissue?

If we believe that all animal tissues are differentiations of portions of the undifferentiated network, the basement membrane must be regarded as composed essentially of a close laminated arrangement of the fundamental filaments, probably coated with some elastic substance, and of "cells" that stand up from it as the energids of this laminated portion of the network, all projecting from one side of it. The arrangement may be regarded as somewhat like that shown in the diagram. Lateral connections between individual energids pass by way of the fibrous membrane. It may be long ere this structure will be recognisable through the microscope, but some of its details are well known. First, there is the root-like attachment of the "cells" to the membrane, which has been familiar to all students of histology. Then, the frequency with which cilia project from the inner ends of these epithelial energids bears witness to the existence of the network underlying them. The cilia, the nuclei, and the root-fibres may all justifiably be regarded as parts of one and the same system. The elasticity of the basement membrane itself also points to its fibrillar texture. This elasticity can be seen on the one hand in the way the membrane stretches round the growing eggs of *Apus* till its energids are hardly visible as the "follicle cells," and, on the other, in its contraction, for we shall probably not be far wrong if we attribute the discharge of the egg into the lumen of the gland as due to such contraction of the membrane and of the networks of the stretched energids.

The protomitomic theory supplies us for the first time, it seems to me, with a good working hypothesis which will account for and link together all these epithelial phenomena. The cell-colony theory makes no attempt at an explanation; the cell is a mysterious entity and we stand wondering at all it appears to do but do not attempt to explain the phenomena, mechanically simple, because we have no data. But once admit that a fundamental reticulum unites all the "cells" into a whole, then naturally the cells composing these epithelia must also be united. Instead of sheets of "cells" resting upon a "basal membrane," we have an elastic membranous arrangement of the fundamental filaments with energids projecting from one of its surfaces, so that the chemical and physical energies of the filaments may be given to the medium into which they are plunged or in the production of which they are engaged.

But we have still further evidence in favour of this explanation of these layers of "cells." For typical epithelia are known which ontogenetically begin as continuous layers of protoplasm with scattered nuclei. Now, to us, a layer of protoplasm with scattered nuclei means simply a laminate protomitomic network. And when this takes on the appearance of a typical epithelium, it does so by the aggregation of large quantities of granular cytoplasm round the nuclei and the projection of these masses above the rest of the surface of the layer. This surely is a simpler hypothesis than to suppose that the cells begin as discrete cells, then completely lose their individuality, and then once more almost completely recover it and become again a layer of discrete cells,—discrete, that is, except for the fact that they rest upon a common membrane.

The Connective Tissues.—Strictly speaking, all the tissues which connect the organs together, whether specialised solely for their support or for their movements with reference to the whole, are connective tissues. I propose to confine myself here, however, to those that passively support the organs and bind them together, and these may be divided into the connective tissues proper (the fibrous and elastic tissues) and the skeleton.

Let us first note that, while there are probably no tissues that have lent such support to the cell-colony theory as epithelia, none have presented so great a stumbling-block to that theory as those usually classed together as connective tissues; the reason for this will become obvious during our examination of them.

The connective tissues fill in spaces, surround and strengthen blood-vessels and nerve strands, support and hold together other tissues, and give the outer skin its real protective strength; they keep the joints and bones in their places, etc. In no case do they appear to be the product of cells which have wandered into the places where they are found, for their substances, in all cases, run on continuously into the fine structure of the bodies they are touching or with which they are functionally associated. There are as many different kinds of cells as of work for them to do. These facts completely baffle the cell-colony theory. Is it not too improbable that rounded, separate cells should have wandered into so many different positions, should have become associated in so many different ways, should have taken on so many different forms and functions, and should now appear in such intimate union with so many entirely different tissues? Harder still is this to understand when we remember that the functions they have had to adopt are most of them purely passive, so that

it looks as if the surrounding tissues must have laid hold of them, chained them, and shaped them to their will, although how and why they should have agreed so as to obtain such a harmonious result is beyond our powers to imagine.

Lastly, those cases in which there are no traces of anything like orthodox "cells," but merely a few stray nuclei, are difficult to reconcile with the belief in the cell as the essential unit of structure.

But while these facts make for the discomfort of the cell-colony doctrine, they could all have been predicted by the protomitomic theory. All these kinds of connective tissue are merely the different forms assumed by the varying remains of the fundamental network—perhaps increased in amount by subsequent growth—persisting between the parts secondarily separated off into organs or specialised into contractile and nervous tissues. They are thus all naturally in direct continuity with the networks underlying the specialised tissues and organs, and they also naturally become differently modified so as to assist in the several functions and activities of the tissues and organs in association with which they are found.

The difficulties in the way of explaining the connective tissues by the cell-colony doctrine are thus cleared away at a sweep by the protomitomic theory, which accounts for the ubiquity and variety of these tissues and, in its turn, receives strong support, not only from the demonstration of continuity they afford, but also from an examination of their finer textures. In their simplest condition, seen in embryos and lower forms, they occur as so many stellate nodes joined by their rays, yielding, indeed, the simplest idea we can have of a protomitomic reticulum such as we have

already seen in a developing Sponge (see p. 91). It is significant for our purpose to note that, though, in their definitive forms, they are always fundamentally reticular, the chief mass of each, in all cases, from the simplest condition to the most specialised, is essentially fibrous. They occur as interlacings of fibrils mostly of extreme tenuity, often rendered elastic, probably by being coated over with other substances, or as bundles of tougher and thicker fibrils which pass continuously into others that have either specialised for muscular contraction or become rigid as bone. Indeed, fibrils of some kind or another in all cases form the mass of connective tissues, while the nuclear nodes may either be simple nuclei or have small varying quantities of cytoplasm massed around them. It is now evident why these tissues have lent so little support to the cell-colony theory. They are largely built of the filamentous elements of the network with few nodes, and these latter contain but little cytoplasmic matter. Epithelia, on the other hand, are composed chiefly of nodes with large masses of cytoplasmic matter around them. The appearance called "cells" is therefore prominent in them, absent in the connective tissues.

These fibrous and elastic tissues do not, however, by any means exhaust the passive support to the complex of organs. The greater portion of the internal skeletal frameworks, of the Vertebrates at least, may be included in the same category, as modifications of the residual portions of the network after the organs have been separated off. A comparative review of skeletons from this new point of view, a review made with special regard to the different needs that have called them into being would, I believe, be of great value.

The Vertebrate Skeleton.—The smallest acquaintance with the structure of human bone is enough to show that it is something quite different from any of the skeletal arrangements found in invertebrate animals. Here, for the first time, we have the appearance of cells as the most striking feature. The protomitomic network helps us, I think, to understand this difference.

After the great mass of the protomitomic network had been used up, as suggested, by the formation of organs and certain special bands and tissues for the support of those organs, a residuum, of course, would remain. It is also obvious that the various binding, contractile, and nervous tissues could not afford sufficient support to a complex of organs without some kind of rigid framework upon which the connecting tissues could hang the organs, and against which the muscles could pull for the movements required for their adjustment. Hence the necessity for the development of skeletal frameworks.

Skeletal matters seem to tend, on the one hand, to coat filaments subject to tensile strains and, on the other, to be deposited in parts liable to pressure. These phenomena are seen throughout life, in vegetable as well as in animal organisms, and must, apparently, be referred to the molecular constitution of the fundamental filaments of the network. The part this tendency plays in the tectonics of organic life has still to be worked out, but instances of it will occur to every naturalist. What interests us most in this connection is the fact that the fundamental filaments which compose a muscle run on continuously into the filaments of tendon and bone. Where the contractility of a fibre ends, the coating with other hardening and strengthening matters begins, culminating in bony deposit. This

is what is meant when it is said that muscles call bones into existence. The strained filaments may become coated with hard matter as the result either of direct pulls on filaments, or of pulls which tend to compress any of the filaments longitudinally. There seems to be no case of skeletal formation to which these principles are not applicable, but though we recognise the principles, we do not yet know enough about them to apply them more than tentatively.¹ There may be conditions, such as the absence of the necessary material for forming skeleton, in which strains have no such effect, and, again, it is not necessary to think that the filaments have no synthetic powers normal to themselves. We shall perhaps be safe in saying that the strains stimulate synthetic energies which are normally present.

Now, with an organ complex such as that of a Vertebrate, in which each organ possesses weight and many require more or less muscular contraction for their functional activities as well as for adjustment (limbs, head, pulmonary apparatus, etc.), there is no wonder that an intricate jointed skeleton came into being, concurrently with the organs and in relation to them, at one spot for protection, at another for support, and at another, again, in response to muscular strains. Such a skeleton, held together in its place by connective tissue which binds the organism into a whole, must evidently be thought of as itself part of the same continuous network out of which the organs and tissues have been shaped, only, in this case, the filaments become coated over with lime salts. It is this last consideration which gives us the clue to the fine structure

¹ It is an obvious suggestion that, as the normal contractile and nervous functions of an organism become enfeebled, these principles might play a part in the production of pathological phenomena.

of the skeleton and explains the appearance of cells which is absent in the earlier skeletal masses. We may, in fact, regard the skeletal framework of a Vertebrate as so many portions of the residual network, the nodes of which are buried in a mass of hard matter, while the filaments, though firmly held, are nevertheless continuous with those of the organs and tissues.

It is obvious, however, that no spicular arrangement due to the coating of stray filaments of this network would suffice for the insertion of powerful muscle bands, and we find a method adopted which is somewhat similar to that employed in the plants, or, better still, we may compare the hardening that takes place round each nucleus with the solid layers of spicules that form the skeletal masses of the stony Corals, only, in the vertebrate skeleton, the filaments running through the prisms run on to the adjoining nuclei. The filaments radiating outward in all directions from each nucleus become coated in such a way as to build up a wall, and each nucleus is enclosed in a chamber or cell of its own, the walls of which thicken and may either be elastic and gelatinous, if the skeletal mass is required to be elastic, or may become impregnated with lime salts if the strains to which the mass is put require it to be rigid.¹

The reader will at once recognise, in the result thus obtained, the well-known histological characters of bone and cartilage with the small chambers or cells each containing an energid and with the intervening

¹ I am not disposed to consider this rise of the skeleton as due simply to the action of natural selection, such as the survival of the fittest out of an indefinite number of different methods and places of depositing skeletal matter. So far as I can see, every gain made by the organism has been a definite response or reaction of the same to some equally definite stimulus.

walls perforated by a network of fine canals. These canals, it is said, are specially visible in the elastic cartilage, when the tissue is inflamed. This is intelligible to us because, at such a time, there would be fuller streams of matter travelling from energid to energid and requiring slightly larger passages through the walls.

This hypothesis as to the building up of vertebrate bone and cartilage masses not only explains why the muscles and the connective tissues are so intimately attached to the skeleton against which they pull, but throws light upon one of the most puzzling facts in connection with the skeleton, puzzling, that is, on the cell-colony theory, viz., the shifting of the position of skeletal deposits during development. It is known, for instance, that the deposits which form the bones of the young are carried away from one part and built up in another in order to form the larger bones of the same shape in the adult. The young child's femur is said entirely to "disappear," the adult femur being essentially new bone. One continuous network having various specialised deposits arranged upon it, might be expected to be able to shift these deposits about according to the exigencies of growth and accompanying variations and shiftings of strains. How, again, could the skull grow greatly in size without a continual readjustment of material? It is impossible to see how cells, as individual units, could agree together to undertake so complicated a process of exchange. But, if the deposits are upon the filaments of a continuous network, and are laid down in response to strains and dissolved away where the strains cease, that difficulty vanishes. Having found that both wall and spicule formation may be due to the activities of the filaments, we have, I think, reason to believe that such

rearrangements of skeletal matter upon the network can take place.

I am aware that far more might be said upon this interesting subject, but my object is not to write an exhaustive treatise. That can only be done when the protomitomic theory has been thoroughly worked out as the cell doctrine has been. I am here trying simply to put together the evidence and indications I have been able to accumulate in favour of the existence of such an underlying network as that which the protomitomic theory demands.

The Muscular Tissues.—It is of no small interest to find that differentiations of the contractile tissues occur which are closely paralleled by differentiations of the skeletal tissues, a fact strongly confirmatory of the reference of both to some common underlying basis. For instance, we have long muscle bands which may be referred to the specialisation of the contractile functions of living filaments, just as we have long skeletal spicules due to the coating with hard matters of long filaments. And again, we have solid masses of the network with its nodes evenly distributed becoming specialised for contraction as a whole, just as we have solid masses of the reticulum in the intervening spaces between the organs of the Vertebrata turned into bone, by the coating of the internuclear filaments with hard matters.

The two kinds of muscular tissues thus yielded may be assumed to coincide roughly with what are called the striped and unstriped muscles, or the voluntary and involuntary muscles, and these I shall now briefly consider, prefacing my remarks by saying that this division is probably too crude and simple.

The involuntary muscles are always in thinner or thicker sheets, and surround cavities of vessels the lumina of which they diminish or increase by their contractions and expansions. Referring back to our protomitomic network, we may imagine a cavity which has arisen in it becoming lined with a layer of energids forming an epithelium. Outside this epithelium we have layers of the network with its meshes more or less stretched according to the degree of distention of the cavity by its contained fluid. The thickness of the network required to contract the cavity will depend upon the work it has to do. There need not be any specialisation of the contractile functions of the ultimate filaments themselves, for the whole mass may contract, as some living Sponges contract, through the elementary contractility of the undifferentiated filaments of the network. It is not the ultimate filaments but the energids that seem to be differentiated, probably in the interest of more gradual and regulated contractions. If the network contracted as a whole, the contractions might be too sudden and spasmodic, but if each energid contracted for itself, a rhythmical, wave-like contraction would be brought about. This result has been obtained by the formation of walls between the energids, so that each seems to be in a separate chamber, the tissue thus assuming an appearance highly suggestive of the cell-colony theory. But, according to the protomitomic theory, these walls are secondary and due to the deposition of matter upon the internuclear filaments about midway between the nuclei, just as the plant cell is formed by depositions of cellulose (see p. 68) and bone cells by the deposition of carbonate of lime on the filaments around the nuclei. In the case of these contractile tissues, the substance

deposited is probably some waste matter, and is required to offer resistance to the contractions of the filaments towards their nuclei, so that each energid may contract and expand by and for itself.

That this is the explanation of the "walls" of the muscle "cells" we gather from the fact that what are called "intercellular bridges" have been seen running between these "cells" and through their walls. It is true that the existence of the intercellular bridges has been strenuously disputed. But such a discrepancy between the observations of different writers is what we have learnt to expect. The filaments, as they pass through the walls in their simplest condition, are always invisible; it is only when coated with matter streaming from energid to energid that they are at all visible. Quite apart from any view as to the existence of the continuous filaments running through the walls being deducible from the existence of the walls themselves and from the contraction of the whole tissue, I should be inclined to argue that, in such massive tissues as, say, the heart, intermittent or periodical streams of nutritive and waste matter must pass from "cell" to "cell." Consequently, since the fundamental filaments are regarded by us as constituting the normal paths for the travelling of such matters from place to place, both those who maintain the existence of the intercellular bridges and those who deny it are probably correct. Some of the observers examined tissues when streams of matter were passing along the filaments, rendering them visible, others, less fortunate, examined tissues when there was no such streaming and the filaments were consequently invisible.

I need hardly again emphasise the advantage of the

explanation of involuntary muscle tissue as originally a continuous network with secondary development of walls, over that of the cell-colony theory, which is compelled to regard it as originally an aggregate of so many separate "cells," which have become secondarily cemented together. It is inconceivable that they should have become cemented together before they began to contract or, on the other hand, that after having begun to contract, any cementing could take place.

A few words more, however, upon the secondary appearance of walls separating the energids. May not these be due to the contraction of the filaments? One half of each filament contracts in one direction, that is, towards the nucleus attached to it, the other half contracts towards its nucleus. Half-way between the nuclei, therefore, there must have been what we may call a dead point in each filament. At that dead point waste matters accumulate and are put to use. We have already seen that where a filament ceases to be contractile it has a tendency to become coated with deposits of skeletal matters (see p. 143). If this is the correct explanation, it may throw light upon the structure of the fibrils of voluntary muscle which we have now briefly to describe from the point of view of the protomitomic theory.

The voluntary muscles may be roughly described as differing from the involuntary in not being sheets or masses of the reticulum with distributed nodes, but bundles of filaments drawn out, often to great lengths, and with the nuclei scattered apparently irregularly along their length. The fine structure of the visible fibrils composing these muscle bundles has long been a matter of dispute. The explanation which

seems to me most probably correct is that which resolves them into contractile fibrils of measurable thickness, showing alternate staining and clear zones, with dark lines running midway across the clear zones. Another view may be mentioned because of special interest to us, although we cannot accept it. This represents the muscle band not as consisting of so many separable fibrils composed of alternate bands, but as a regular network of parallel filaments and cross junctions. These networks are regarded as peculiar specialisations of the spongionoplasm or fundamental network underlying the muscle "cells." This view, in spite of the support it appears to give to the continuity of our hypothetical underlying network, I am unable to accept because my own observations are not reconcilable with it. It is true that the spongionoplasm (*i.e.*, the fundamental network) plays a great rôle, but it is a different rôle from that suggested. Besides the parts of the network forming the basis of specialised contractile fibrils which run through the "sarcoplasm," there must, of course, be other parts joining fibril to fibril and all the fibrils to the network of the nuclei. Others, again, must keep the whole of this highly differentiated reticulum of the muscle band connected with the rest of the organism. Among these latter fibrils may be mentioned those that run to the nervous system, those in connection with the networks underlying the blood-vessels, and, lastly, those which attach the muscle at each end to its point of insertion. These latter would be primarily direct continuations of the filaments underlying the contractile fibrils, but portions which no longer contract, being coated with hard matters to form bone and cartilage.

Assuming, then, the existence of these highly special-

ised contractile fibrils differentiated though not separated from the ordinary reticulum, what explanation can the protomitomic theory supply of their finer structure? In the first place, they are far too thick to be regarded as single filaments unless we could imagine them to be very thickly coated with other matters. This is unlikely for, though such coating might strengthen the filaments, it would not increase, but rather diminish, their contractile power. In order to attain to efficiency in these respects, the simplest course is surely to multiply the filaments themselves. And there is no difficulty in regarding each of the contractile fibrils that compose a muscle band as a bundle of elementary filaments.

This conception is a clear gain and it seems to me that, by the aid of what we have learnt from the mechanism of the involuntary contractile tissue, we can find a possible explanation of the remarkable cross banding of these wonderful fibrils. Every division or compartment, from black line to black line, may be regarded as a minute energid; the black lines are analogues of the walls against which the filaments contract, the clear zones are bundles of naked and invisible filaments, the staining bands represent filaments coated with chromatin substance; and it is towards these bands that the naked filaments contract, just as, in the energids of the involuntary muscle, they contract towards the nuclei. Each compartment being a cylindrical bundle of filaments, the black line or wall is only needed as a plate between the different compartments, whereas, in the involuntary muscles, in which the pulls are from all points towards the nucleus, the wall has to envelop the whole energid.

There are several other considerations besides the

formation of the black lines which help to confirm this view. For example, it seems to offer an explanation of the enigmatical collodium impressions of muscle fibrils discovered by Prof. Haycraft. Each impression looks, under the microscope, indistinguishable from the real thing, except that it shows no staining. Now, it seems to me that, if the fibrils were constituted in the way above described, just such an impression would be given. The clear zones, being bundles of naked and invisible filaments of exquisite delicacy, would leave no mark at all, but the black lines would mark, because each filament is coated at that spot with some hard matter, so that the filaments together form a hard disc, and, similarly, the staining bands would mark, because the filaments, at those places, are coated or involved in some way with chromatin. Only at the parts where the filaments are thickened by other matters can the fibrils make any impression on the collodium.

Two more points are also worth calling to mind; both tend to support the suggestion we are now making. The contractile energy seems to depend upon the naked fibrils contracting towards the chromatin in the staining band. Now it is known that each compartment contracts by the clear zone apparently disappearing into the stained portion, and it is now also known that when, after repeated contractions, the muscle is tired out, the stain is no longer in sharp bands, but diffused over the whole compartment. This we should interpret as meaning that, when chromatin has spread over the zone of naked filaments, the power of contraction has ceased. What the nature of the contraction towards the chromatin is it is as impossible to say as it is to account for the nature of the nerve

stimulus. We have to fall back upon our imaginary hypothetical unit, a single chromidium with its radiating linin threads, one of the elementary vital phenomena of which is the power the threads possess of contracting back toward their chromidial centre.

The other point is as follows. It is sometimes found that the long staining zone has a white clear band across it. This we must also think of as a place where the linin filaments are not coated over or in any way involved with chromatin. It seems inevitable that, here also, since one half of the compartment is pulled one way and the other half the other, there must be a zone of dead points across the waist of each compartment. Hence we might expect to find a disc of matter collecting, and this, indeed, is what we do find. In what is probably the most specialised contractile tissue in the animal kingdom, viz., in the wing muscles of the common bluebottle, whose alternate contractions and expansions are of almost inconceivable rapidity, we find a pronounced dark zone across the middle of the compartment.¹

It is not only clear that all these points hang together, but it is also obvious that, given the elementary fact that the filaments of the protomitomic network seem always to contract toward the nuclei (*e.g.*, in the *Amœba* or in the energid of the involuntary muscle), we have, in such a muscle fibre as has been here described, a perfect mechanism for the adaptation and utilisation of this principle. Each fibril is a long bundle of filaments, coated at each end where it passes continuously into the solid bones which have to be pulled against, with hard elastic substances, while, at intervals,

¹ See "On the Relations of the Isotropous to the Anisotropous Layers in Striped Muscles, *Zoolog. Jahrb.*, 1893, p. 359.

along the whole of the middle portion, the filaments have bands of chromatin into which the naked portions contract. The contractions begin at one end of the fibril and travel like a wave along it, so that the increase in the tension is graduated and not sudden and tearing. Indeed, we could imagine each fibril to be a very thin, string-like arrangement of energids like those of involuntary muscle, only, as the strains are always in one direction, the "walls" are merely required to be disc-like divisions between the separate cylindrical energids. It would be difficult to imagine an arrangement more simple or more efficient for the purpose of obtaining the precise and definite pulls of large amount in definite directions which are necessary for the movements of a highly specialised skeletal mechanism.

Nerve Tissue must be left for consideration in another chapter. Nerves differ from both muscles and connective tissue in that, while the latter are functionally confined to the spots where they occur (though, of course, the filaments themselves run on continuously under different forms into the adjacent tissue), nerves continue as nerves right into the organs on the one hand and toward the central nervous system on the other. They cannot, therefore, be profitably treated merely as bands connecting the organs with the main body; the nervous system has to be treated as a whole.

CHAPTER X

THE EPIDERMIS AS A MODIFICATION OF THE OUTERMOST LAYER OF THE PROTOMITOMIC NETWORK

THE internal tissues so far called upon to bear witness to the truth of the protomitomic theory may, with the exception of the skeleton, be called the *fibrous* tissues. Each in its own way shows that it may be merely a differentiated part of a continuous fundamental reticulum, the filamentous elements of which have been utilised and developed for special functions, contractile, elastic, suspensory, or conductive of nerve stimuli.

There are other tissues, however, in which not the filaments but the nodes of the network are specially developed. The filaments here, though necessarily taking an active part in the vital functions, do not receive any strong emphasis as filaments, for the functions of these tissues are mainly metabolic and secretory. Of these tissues, which may be classed as *glandular*, the epidermis, the liver, the kidneys, the lungs, and the reproductive glands are examples.

In this chapter, I propose to confine my attention mainly to the epidermis, because its evidence is obvious and far reaching. Indeed, if the whole covering of the body can be shown to be but a modified outer layer of the protomitomic network, such a witness will rank with the nervous system itself in the weight of its

evidence. If these two tell the same tale, as we shall see that they do, further evidence would appear almost needless.

Before dismissing the rest of the glandular structures, however, and leaving them to be brought into line by other workers, I would draw attention to one very remarkable specialisation common to three of them: the lungs, the liver, and the kidneys, which show three stages of complexity very difficult to account for on the cell-colony theory.

In the lungs, we have air passages and blood passages, in the liver blood passages and gall capillaries, and in the kidneys blood passages and tubules which carry off the urinary secretions and together form complicated tangles. In a continuous reticulum with fluids flowing through its meshes, the formation of such intertwining systems of tubes is merely a question of the secondary increase and arrangement of elements already present and capable of functioning in the way required. Each system began in a rudimentary way, a whole from the first, and in direct vital continuity with the rest of the organism, and has only required to be specialised. The cell-colony theory, on the contrary, has to assume that so many independent "cells" fall into line to build up the tubes and give up their whole life-activities to one special function, and that this takes place in each case in advance, for the tubes have to be formed ready for the duties they would have to perform. In the one case, the streams existed in a continuous tissue which became modified to deal with them, and in the other, the mass of separate and similar cells arranged itself and underwent the necessary individual modification beforehand in order to deal with the streams which it would some day find flowing through it!

An indirect argument in favour of our theory is thus afforded.

Of more direct arguments as to the origin of these glandular tissues from a fundamental network we may note that the bronchial tubes leading from the lungs are ciliated; that the filaments continuous with the nerve fibrils have been seen running towards the nuclei in the walls of the tubules of the salivary glands; that the flagella of the spermatozoa produced in the male reproductive glands proclaim them to be small protomitomic networks (see p. 74); and lastly, that the frequent mitotic divisions seen in the reproductive glands demonstrate beyond doubt the presence of the fundamental network, as we shall see in Chapter XIII. Other evidences might doubtless be adduced, but we must now pass on to show that the epidermis is essentially the outer layer of a protomitomic network. We have to demonstrate how the skin formations found in the Metazoa can be referred to the outermost fringe or layer of such a reticulum variously modified, and, in association with the outer covering, we shall consider the linings of the internal passages, which may also be regarded as surfaces of the body.

The normal surface of a three-dimensional reticulum, increasing in size by the growth in length and branching of its filaments, might be expected, as already noted, to be a fringe of free filaments which, by their vibrations might serve as locomotory organs for small aquatic forms. But such delicate vibratile organs, or cilia, would hardly persist as external organs, even in aquatic forms, after a certain size was reached, for not only would they be useless as organs of propulsion of the larger body but the delicate skin usually associated

with the protrusion of a cilium, even if strengthened by subjacent fibrous tissue developed in order to protect and support the organs of large complicated forms, would probably be too sensitive to external impacts and changes of environment. Surface cilia would paralyse the function of the central system for all co-ordinated action. In the larger Metazoa, consequently, it would only be in internal passages, *i.e.*, in parts sheltered and kept moist, that cilia might be expected to persist and there they are found, occurring, indeed, in such places with sufficient frequency and variability to justify us in claiming their presence as due not to so many independent spontaneous developments of different "cells," but to the fact that they express some fundamental texture of the whole organism. Other internal surfaces, though they have no cilia, have what are called "striated borders," which, there is reason to believe,¹ are the homologues of the cilia and which, as they do not project freely beyond the surface, may be regarded as the roots of cilia. The tale they tell is the same for our immediate purpose. That these "borders" are considered to be contractile is what we should expect, inasmuch as the protomitomic filaments are primitively both contractile and responsive to stimuli.

Since free cilia are no longer found on the outer exposed surfaces but only in the internal cavities and passages of the larger forms, the interesting question for us is, what do we find at the outer surfaces? The answer once more is in perfect harmony with our evolutionary sketch. We have a repetition of what happened in the case of the protoplasts, where forms that required protection developed skeletons, in all cases, by the simple

¹ Vignon, *Arch. Zool. Exp.* IX, 1901, p. 371.

method of coating the free cilia with various matters, the whole thus receiving a covering in the shape of a compact layer of rods arranged side by side. If these were hard and fitted tightly together, the protoplast was covered with a rigid skeleton; if soft and able to slip against one another, the covering was like that of the *Amœba*. Precisely similar processes seem to have taken place in the case of the Metazoa. The conditions differ, however, in the fact that the networks are larger and, with all their associated fluid and albuminous contents, much heavier. In both cases, the surface consisted of the fringe of filaments. When the free, vibratile ends of these ceased to be of any use to the Metazoa, the method of coating themselves over with some skeletal substances was always available, and this is what every larger metazoan without exception has done, though in several different ways.

We may also note that, since a thin, continuous hard covering would be impossible round a heavy body that had to be capable of locomotion, the protective covering was, originally at least, flexible. Such a covering is supplied by chitin and we find that a thin chitinous covering was developed by the Annelids, where it still persists, and by the Molluscs where, however, it persists only in the periostracum outside of the shell.

I am not aware that there is any actual evidence at hand to show that this thin flexible chitinous layer, say in the Annelids, is built up at the tips of the filaments, but such evidence can be found where the layer has been greatly thickened. For, in time, the originally uniform layer became differentiated. At the regular bending places of the body, it remained thin and flexible but the stationary parts to which the muscles were attached thickened and became rigid. The

Crustacea, the Insecta, and the Arachnida, which are all three descendants of the Annelida, show three distinct differentiations, all taking place on the same principle but with different results in accordance with different methods of life. In the Crustacea, the filaments bring carbonate of lime still further to stiffen the chitin. In the Insecta and the Arachnida, the chitin is stiffened in the most rigid parts by becoming extremely dense. It was in studying one of the Arachnids (*Galeodes*)¹ that this method of skeleton formation was first revealed to me.

Sections of some of the thicker masses of chitin which protect the thorax of *Galeodes* show (what is well known) that the chitin is laminated and that the thicker, inner layers

are softer than those nearer the surface (Fig. 26). The outermost layer is hard and brittle and refractive and might, as I have suggested, be called the glassy layer. Under a high power, this glassy layer is finely striated perpendicularly or slantingly to the surface, at least on its inner side. It is difficult to ascertain whether

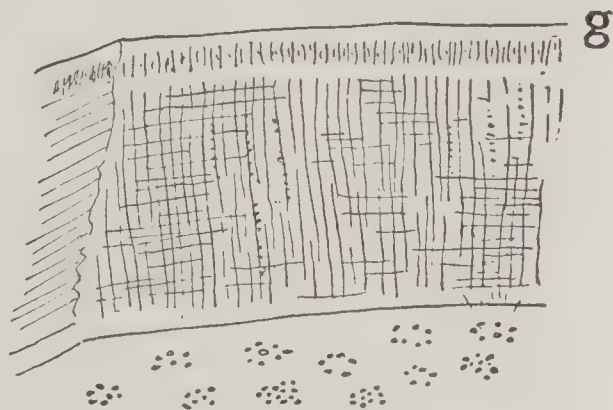


FIG. 26

Thick portion of the cuticle of *Galeodes*, showing the outermost, refractive or glassy layer (g) followed by many layers of softer laminated chitin, traversed by canals containing deeply staining protoplasm and pigment. These canals terminate in the glassy layer. The hypodermis cells have broken away, leaving small groups of deeply staining points, which are the proximal ends of the protoplasmic processes traversing the chitinogenous layer.

¹ *Comparative Morphology of the Galeodidae*. Trans. Linn. Soc., London, vol. 189, pp. 330-331, pl. XXIX, Fig. 15.

the striæ reach the surface. Where the thicker, softer layers are more developed, what have been called the chitinogenous "cells," that is the layer of energids whose immediate filaments deposit the chitin, are frequently no longer demonstrable. I was, however, fortunate enough to find, in *Galeodes*, a layer of nuclei closely adhering to the inner surface of a portion of the chitin and sending fine staining processes far up into it. These processes tapered away into invisibility and, though embedded in the chitin, were superficially suggestive of long, staining cilia. Where the nuclei had been torn away, these staining processes could be seen as groups of dots on the under surface of the chitin. But, while they gave the clue to the striæ of the glassy layer, they were themselves at the time enigmatical, especially coming, as they did, direct from the nuclei. The protomitotic system has now rendered them, for the first time, intelligible. We see in them, indeed, exactly what might have been predicted according to that theory.

There is, however, one point in the description of the formation of the thick chitinous layers of *Galeodes* and *Scorpio* that requires settling. Is this thick deposit entirely built up round the filaments of the surface fringe, or is not some part of the reticulum involved as a reticulum? May not the glassy layer, with its striæ, represent the layer of free filaments, and all the thicker layers be laid down upon the filaments in such a way as to involve several layers of meshes?

The fact that the chitin is laminated need not necessarily imply this latter supposition but, inasmuch as pigment granules which appear to be always associated with the filaments are found in the solid chitin, spread out between the layers parallel with the surface, we are, I think, justified in concluding that cross filaments

also run between these layers. If so, we may surely believe that at least the thick layers of chitin are laid down by the outermost layer of the reticulum as a reticulum, and not merely on the fringe of filaments.

We may thus provisionally regard the striæ of the glassy layer as due to the tips of filaments like so many cilia embedded in this refractive, brittle substance. Whether they end *in* this layer or form small openings at its surface I have not been able to ascertain. That they do at times protrude beyond the general level of the glassy layer may be gathered from the fact that at certain spots, *e.g.*, at the slit-like apertures of the tracheæ through which the air for respiration passes, structures may be



FIG. 27

Longitudinal section through a cephalothoracic stigma of a Rhax. The setæ modified to form a protective sieve. The flat-headed hairs within the aperture appear to be open at their tips, and may be olfactory.

found which would be difficult to account for on any other hypothesis. Fig. 27 represents a longitudinal section of one of the tracheal openings in the cephalothorax of Rhax. The glassy layers are seen to rise up into flame-like spikes, together forming a network. In addition to these there are simple flat-headed processes which appear to have apertures at their tips and where exposed ends of the protomitomic filaments might well be found, functioning perhaps as olfactory hairs. These upgrowths of the glassy layer may be compared with

those from the surface of the shell of the Mollusc *Spondylus*, both being due to growth in length of the protomitomic filaments which carry along with them the material for the building up of the skeletal surface. In neither case can they be built up by "cells."

Now, if we are justified in assuming that what can be learnt from the Arachnids is applicable to all chitinous cuticles, we shall have the fringe, with or without a layer of meshes of the reticulum, established as the vital factor in the construction of the outer coverings of the whole of the Arachnida, the Annelida, the Insecta, and, we may add, the Crustacea. In these last the protomitomic filaments, in addition to chitin, bring calcareous matter which renders the covering specially rigid.

The epidermis of the Vertebrata differs from that of the Invertebrata in the fact that not only one simple layer but many layers of nuclear nodes are given up to the production of the chitinous or horny covering. Seen through the microscope, its appearance lends great support to the cell doctrine, since the individual "cells" are most distinct, each with its nucleus and its cytoplasmic cell-body. It, however, presents one variation on ordinary tissue in that the cells are all joined together by short strands or "cell bridges" and, when teased out, parts of the broken bridges stand out all round the cell in a way which has given rise to the name of "prickle cells."

Many have been the attempts to account by the cell doctrine for the so-called prickle cells, *i.e.*, to account for the "individuals" constituting this particular tissue having become joined together in so remarkable a manner. Some have thought that the "cells" have

been forced apart and that the bridges are the strands of the torn membranes. Heitzmann, however, rightly claimed them as evidence for his doctrine of the structure of protoplasm as a continuous reticulum¹; not only, however, did he fail to show that any other tissue had such bridges but he was unable to formulate any clear doctrine of that reticulum. These unique bridges were to him filaments of the reticulum. Others, however, came closer to the truth and maintained that the threads of the fundamental reticulum passed *through* the bridges (Ranvier, Ramon-y-Cajal and others).

I have elsewhere had occasion to describe the so-called "cell bridges" which are seen between some cells and not between others. In no other known tissue except the epidermis are they permanently visible, the reason being that in no other known tissue

¹Heitzmann, in his *Microscopical Morphology*, published in 1883, endeavoured to show that many facts of histology could be interpreted in this way and that, in general, the reticular system which he assumed to be underlying the whole could, by various simple modifications, be made to account for the development of all known tissues.

As a matter of fact, indeed, his theory appears to have given a few apparently accurate accounts and explanations; for instance, he figured the nuclei suspended on strands which run into the "cell body," and in this cell body the filaments join the cytoplasmic portion of the network; he even proposed to account for cilia as the projection, beyond the external surface, of the free ends of the threads which compose this network. Indeed, further, his assertion that every nucleolus is a prickly nucleolus and his figures of these may be taken to indicate that, without attempting to formulate his view, he dimly perceived a unit of structure identical with the hypothetical unit described in Chapter I of this work, viz., a single chromidium with its linin-chromatin rays. But, as a whole and in spite of these few cases of insight, Heitzmann's network has failed to carry conviction. The reason is that, although Heitzmann protested against the "cell" as the unit of structure, he still could not himself get far enough away from it. It still, as a

are streams of matter always passing through from cell to cell. Such transmissions are, as a rule, periodical, and it is consequently a chance whether the fundamental filaments are visible or not. This is the explanation of the contradictory observations which have been recorded as to the existence or non-existence of the fine fibrillar connections between so-called "cells" and parts of cells.

In the epidermis of Vertebrates, there is a perpetual stream of waste matter passing outward to form a protective covering to the body. This is indeed the rule in all organisms whether large or small, whether an *Amœba* with soft matter coating its filaments and forming its exoplasm, or a Foraminifer whose filaments build up its calcareous shell, or a plant with its cellulose wall also built up by the filaments, or a Metazoan with its outer covering built up by the matter

"territory," continued to obscure his view, even blinding him to the teaching of his own diagrams. Further, his doctrine was not explicit enough. "Every cell," he declared, "is a prickle cell," which means that every mass of cytoplasm is united by cytoplasmic strands with every other mass; "every nucleus is a prickle nucleus," but what was the nature of the strands which unite the nuclei to the cytoplasm? Lastly "every nucleolus is a prickle nucleolus,"—what again are its prickles? He figured his fundamental reticulum as regular, homogeneous, and coarse with microsomes—his "prickle nucleoli"—at the nodes, and with its meshes spread evenly and continuously through both the nucleus and the cell body and joining all together. Over this reticulum, the orthodox cells are marked out, only they are called "territories" instead of cells. In this diagram he comes nearest to the protomitomic theory; indeed, what he sketched would have served as a very coarse representation of the actual reticulum had he made the "prickles" of the nucleoli and nuclei running *through* the prickles of the territories as through tubes, had he, in fact, made his network a nuclear network in which his territories were as masses of matter aggregated round the nuclei and in the meshes of the network. But Heitzmann's scheme was a mere, shall I say, conjectural outline. It was conjectural, for he had not sufficient evidence, and it was an outline because

which streams outward, coating its filaments on the way in order to harden at the surface. This is the keynote to the understanding of the vertebrate epidermis.

Let us first take the best known, and, at the same time, almost the most complicated epidermal tissue, that of Man. The streaming material passes through a considerable thickness of the surface network involving many layers of nuclear nodes, and necessarily considerably modifies the texture and arrangements of the filaments. Some years ago, before I had any knowledge of the continuous network underlying all organic structure, I made a comparative study of skins, in connection with my endeavour to deduce the vertebrate eye from the skin, and with the special view of discovering the fate of the pigment in that tissue. I then became convinced that streams of waste matter

he could not fill in any of the detail. The continuous reticulum is there and, in the diagram, it is the all-important thing, but he made no attempt to explain either what the three kinds of bodies, fitted like Chinese balls inside one another (the cytoplasm, the nucleus, and the innermost nucleolus), were, nor what he considered their physiological relationship to one another to be. While he disputed the existence of cells in words, he left us with still more mysterious "territories." We had some intelligible doctrine of the cell; he gave us none as to these complicated but shadowy blotches upon the all-important reticulum. His doctrine thus failed, not only because he could not reconcile it with facts, but because it was not worth any man's while to take it seriously. It was altogether too vague. His chief failure is not being able to show what were the relations of these three components of his territories to the fundamental network. It is in this very point that the protomitomic theory has succeeded.

While, then, the continuity which Heitzmann proclaimed does certainly exist, it does not exist exactly as he described it. The continuity, it is true, has a network at its base, but it is not a cytoplasmic network but a chromatin-linin network with cytoplasm massed in varying quantities round the nuclear nodes.

One further limitation must also be made to these admissions.

were at all times passing outward towards the surface, their course being revealed in wavy lines which, I noted, always seemed to avoid the nuclei, in that they bent round upon the surfaces of the "cells." In crossing the interspaces, they seemed to form the cell bridges. From cell to cell, they pursued a wavy course in such a way as to form a kind of shell of interlacing streams round each "cell." Within this shell was a thin layer of protoplasm and within this a clear space containing a gradually shrinking nucleus. I was sometimes able to follow the continuity of individual streams over two or three cells at a time in sections of a human tongue that had been fixed in a highly inflamed condition.

It is obvious that, as soon as the protomitomic network came into view, the mysterious continuity of these streams was explained. The matter was merely finding its way along the filaments of this network. It did not form the cell bridges but only revealed the

Heitzmann held that the fundamental reticulum passed continuously through the whole organism, even joining organ to organ in one continuous mass. It seems to me very obvious that any high development of special organs capable of movement with reference to one another is not possible on this assumption. All we require is organic continuity and not such a complete and absolute physical continuity as Heitzmann seems to have imagined. The organic continuity required by the protomitomic theory can be maintained if the portions of the network which are being specialised as organs become separated off only partially by the rise of lacunar spaces, the organs themselves remaining connected with the rest by bands and filaments specialised into connective tissue, muscle, or nerve strands. And this is what we find, for these three are always present, in varying proportions according to the special functions of the organ. It is possible that I am exaggerating this difference between Heitzmann's doctrine and that here stated; still I cannot help thinking that Heitzmann's words are a little misleading and that we get a truer notion of organ formation in the way suggested by the protomitomic theory.

presence of otherwise invisible filaments by thickening them. There is no knowing whether the individual streams are able to change their courses (a network presents them apparently at all times a choice of routes), or whether separate paths are established, the guiding filaments of which become specialised for the purpose. This latter view is more in accordance with the laws of evolution.

So far we have described the streams but have brought no actual evidence for their existence; we have been arguing simply from the analogy of other organisms. Some evidence comes to light, however, when we note that the matter of the streams, as it crosses the cell bridges, may, under the action of reagents, shrink together and form a small swollen mass in the middle of the bridge which is connected with the energid on each side by a filament of extreme tenuity. This phenomenon has already been described in connection with *Volvox*.¹

But still more conclusive evidence is found where the streams get near the surface; the material accumulates and has to be disposed of. The first trace of this is seen in that it appears to leave the special paths along which it has travelled and presumably overflows on to the side filaments which run into the energids. The layer of the energids, where this takes place, naturally becomes granular in appearance and is called the *stratum granulosum*. These granules are the drops and masses of the material upon the network of the energid between the outermost layer and the peri-nuclear space.

The next stage is interesting because it shows these

¹The usual tendency is to regard these swellings as normal and, when not seen, as a matter of staining. My experience does not support this view.

masses of matter apparently deliquescing and running together into a homogeneous clear matter which almost fills the energid with the exception of the nuclear cavity. The layer of these energids is known as the *stratum lucidum*. This homogeneity is not again lost, the next change being apparently a hardening of the whole into horny matter, each energid consequently becoming a minute horny scale. The scales are all bound together by the connecting filaments of the network, probably strengthened by a thin coating of horny matter.

This is not all, however, that we can gather as to the gradual arrival of waste matters at the surface of the body, and of its transformation into horn. Two other influences can be noted as doubtless helping in the transformation. For instance, as we saw above in the description of such a thick chitinous cuticle as that of *Galeodes*, the nuclei here also must take an active part. In that cuticle, filaments could be seen running into the chitin directly from the nuclei, but the nuclei nevertheless gradually empty of all chromatin contents and degenerate. In following the streams carefully outward, we note that, in running on the outer surfaces of the energids and crossing the "intercellular" spaces, they are not only all the time being bathed by the fluid in these spaces, but are also at all times in fibrillar connection with the nuclei. Filaments actually running to the nucleus are difficult to see because they are only occasionally coated with matter leaving the nuclei to join the streams. That this is their destination we gather from the fact that this connection between the nuclei and the surface with its bridges can be seen at any time in a young tadpole.

The actual phenomena here referred to have been fairly well known for some time, but the interpretation

here given, the essence of which is the streaming of waste matter along the filaments of the continuous reticulum, is new. That this interpretation gives a simple and intelligible meaning to the phenomena is in its favour; it also fits into its place in the whole scheme founded upon the mass of demonstrable facts contained throughout the rest of this work. It is, further, confirmed by a comparative study of vertebrate skins. In some of the lower forms, the filaments still end freely at the surface as a fringe, but, inasmuch as the material for the production of horn streams along them to the surface, we ought, according to our view, to find these free filaments coated at the surface with horny matter, and this is exactly what we do find.

In *Amphioxus*, the epidermis consists of a single layer of energids at the outer surface of which there is a fringe of filaments stiffened by horny matter and, again, in the Hag-fish, where the epidermis is many-layered, with typical "cell bridges," the outermost energids have dense brushes of horny rods or bristles at their external surfaces. Now, quite apart from our theory and in view alone of the almost universal presence of cilia at the external surface of primitive animals, the suggestion would be unavoidable that these stiffened bristles are the homologues of cilia, that is, that they *are* cilia coated over and stiffened by horny matter. This suggestion is entirely in keeping with the scheme of evolution outlined in this work.

Let us take one more example. In the young Tadpole, the material collecting at the surface energids not only runs out on to so many free filaments, but hardens *in situ* as a continuous plate or cap. The filling up of whole energids with horny matter and their perishing

as dry scales is only a further stage of specialisation adapted to the needs of the organism. One such need may be noted in passing: that of producing a strong and efficient skin and yet one capable, at the same time, of continuous extension so as not to impede growth—one, in fact, which would avoid the dangerous process of shedding the whole skin at once. This problem is solved by the constant shedding of minute portions which are as constantly replaced, more being produced or fewer as wanted.¹

These various arrangements and specialisations of the horny matter at the surface all hang together and are all referable to the same principle; the synthetic functions of the filaments of the fundamental reticulum bring waste matter in endless streams to the surface of the body, where it may harden on the filaments and project as bristles, or else form a continuous cap or cake distally to each energid or, again, form so many nearly separate scales by enveloping complete energids.

This is perhaps the place to note what appears to me to be an interesting sidelight upon the streaming of the material along the filaments. It has been stated by Flemming that, when leucocytes or certain of the free protoplasts, which wander within the meshes of the network of all the larger organisms, squeeze their way between the energids of the epidermis they destroy the cell bridges which, however, form again as soon as they have passed. The destruction of such fundamental structures as the linin filaments with their vital functions hardly seems so probable an interpretation

¹ The Snakes seem to have returned to the habit of ecdysis or sloughing. The friction incidental to their method of locomotion has perhaps modified their skin into a nearly continuous horny sheath, which can only be got rid of in one piece.

of the phenomena as that the leucocyte, in passing, absorbs the matter coating the filaments, thus rendering them temporarily invisible. They appear again as soon as the streams are resumed.

One word as to the fate of the pigment which was the object of my early researches. Being discharged into the skin, it was bound sooner or later to be involved in the streams we have been discussing. In the skin of a negro, I frequently noticed pigment granules on the bridges of the energids. When *in* the energids, they were most frequently found at one of the tips, proximal or distal, sometimes at both. One or two at a time were seen on the longer bridges at such tips. This association is not new, for pigment granules have already been seen in close association with the contractile filaments of a chromatophore (see p. 62, Fig. 5) and we shall find them again later on in the same association in Chap. XII. What is new is to find them on the filaments carrying streams of waste matter, leading to the conclusion that they also are waste matter. We may perhaps gather from the fact that albinos are reputed to have very delicate skins, that the pigment forms an important constituent in the material which becomes transformed into horn.

We pass on now from the epidermis itself to its characteristic structures, Hair and Teeth. As to the first of these I have little to say except that, on the very face of it, such long, horny, and frequently deeply pigmented filaments projecting beyond the surface of the body do not seem so difficult to understand according to our theory as according to the ordinary cell doctrine. Streams of matter being conveyed to the surface along fundamental filaments of the network, and filaments capable of growth supply factors obviously

capable of producing hair. The premature drying and hardening of the horny matter upon any sufficiently large bundle of the filaments might account for the original start of a hair. Its own growth at its base would cause the hard mass to thrust against the external surface layers through which it had to burst its way. This thrust could easily give rise to the projection of the hair-producing part of the epidermis as a flask-shaped process into the cutis below, with the obvious result of intensifying and compressing the stream through the neck of the flask. Such structures as hairs would almost certainly be produced in a covering like that of the mammalian epidermis, for it seems as if they could result merely from inequalities in the consistency of the waste matter. Spots where, for some cause or other, either from the nature of the material or from the diminution of the fluid in the interenergidal spaces, the skin hardened too soon, might produce hairs. Pressure such as that of a boot may well, by diminishing the amount of this fluid, cause the painful concretions called corns, but for hairs we must look to much finer causes, to minute areas of lesser supply of fluid, or greater supply, say, of pigment. Perhaps different causes will be found to account for the different characters of hair on one and the same body; the hairs of the head, as we know, may be exquisitely delicate while those on other parts of the body are coarse. These, however, are but suggestions, introduced merely as illustrations of how our theory may supply us with working hypotheses for analysing and classifying organic structures.

One other illustration of this kind is afforded by the spines or hairs which spring up from the chitinous covering of an Arthropod. Fig. 28 shows a typical

spine of an Arachnid inserted where the chitin is not very thick and where the layer of energids is demonstrable. The glassy layer described above is continuous over the spine, the core of which is of softer chitin. A group of deeply staining filaments runs from the layer of energids to this softer chitinous core. It is possible that, occasionally, there may be a nuclear node on the butt end of a spine, but I do not remember ever having seen one. The thickness of the filaments attaching the butt end of the spine to the soft chitin of the surrounding skin and their deep stain show that they are coated with material which they convey into the axis of the spine, round the periphery of which it hardens into a glassy layer exactly similar to that of the rest of the surface. Both this Arachnid spine and the Echinoid spine are sudden, flame-like projections of the filamentous reticulum; in the one case the filaments carry out chitin and produce a chitinous spine, and, in the other, calcareous matters which form a calcareous spine.

Again, as, in the calcareous spine of the Echinoid, the filaments at the base are variously specialised, some for conveying matter, others as elastic ligaments, others, again, as contractile bundles, so in this Arachnid spine there appears to be a ring of fibres which might



FIG. 28

Method of suspension of a hair of Galeodes by the glassy layer which also forms the outer covering of the hair and lines the chamber in which the butt end is suspended; this end is attached all round by a ring of radiating and deeply staining fibres.

be contractile and serve for its erection and depression in different directions.

But these, again, are mere illustrations of the possible applicability of the theory. Too little is yet known of the exact structure of the objects themselves for us to feel certain whether it supports the theory or suggests difficulties.

There are, however, characteristic organs in the skin which, in their structural features, show unmistakable evidence of the protomitomic network and of the synthetic activities of the filaments. I refer to the Teeth. The ontogenetic development of these organs throws little light on their phylogenetic development. We dimly gather that hard, bony nodules must have formed, probably under an epidermis consisting of a single layer of energids, and that the pressure put upon these nodules by use drove them deeper and deeper into the tissue almost as fast as they grew, until a condition of equilibrium was reached. In the ontogenetic development of the tooth, we see some reminiscences of this process of sinking in the downward growth of the enamel organ.¹ In the structural details of the tooth itself, we appear to have the bony mass still preserved in the dentine and the representative of the original epidermis is perhaps found in what are known as the enamel cells and their hard secretion of enamel which form a cap over the tooth. I am not specially concerned with the exact correctness of these homologies; it is possible that the protomitomic theory may some day help us to establish them. I am here most interested in calling attention to the striking traces of

¹The process has probably been confused by the fact that, since the first appearance of the tooth, the epidermis may have changed from a single to a many-layered arrangement of the energids.

the fundamental filaments afforded by both the enamel and the dentine.

Taking the Enamel first, close analysis shows it to consist of a compact mass of extremely delicate calcareous prisms arranged side by side, together forming a layer of extraordinary hardness. This at once recalls the layers of calcareous prisms which form the skeleton of the stony Corals and which supply the chief constituent of the Mollusc shell. The calcareous matter streams outward along the filaments on which it hardens and, when these filaments are arranged as a dense fringe, the hardening of the matter upon them turns the fringe into a hard, skeletal layer. In the case of the coral skeleton, we were able to homologise the filaments coated by the calcareous matter with the cilia so common at the surface of these lowly forms. In the Mollusc shell, the filaments are the dorsal ends of those which, ventrally, formed the contractile bundles of the great dorso-ventral muscles. In the stiff rays of protozoan skeletons, we have analogues of these prisms, free or grouped in ways very different from that in which the compact layers of enamel are built up.

In the Hag-fish, filaments can be seen coated with hard matter projecting side by side like the bristles of a brush. Lastly, in the enamel organ, we have filaments conveying the streams which run out through the epidermis.

The finer details of the structure of the Dentine are



FIG. 29

Diagram of three Odontoblasts, with their anastomosing processes in the dentinal tabules, *d*, dentine; *o*, odontoblast.

of still greater significance. Here the material, which is softer, having more organic matter mixed with the lime salts, is no longer arranged as excessively hard prisms built round so many parallel filaments. Close examination has shown it to be traversed through and through by a fine reticulum of living threads(Fig. 29).¹ This reticulum is part of the protomitomic reticulum,—an outer layer of the general reticulum of the papilla or pulp of the tooth.

The reason for this abrupt change from an enamel deposited upon parallel filaments to a dentine deposited in the meshes of a network is at once clear if we glance back, for a moment, at the sketch given above of the origin of the tooth. The parallel filaments and this network represent respectively the surface fringe and the portion of the network to which it once belonged. The waste materials came to the surface and, where teeth are found, seem to have stagnated on the network as dentine, the fringe having only carried away so much as has turned it into a hard layer of prisms. From this point of view it seems necessary to assume that, at one time, the underlying filaments which build up the dentine ran on continuously to form the fringe which deposits the enamel. This does not now appear to be the case in the ontogenetic development of the tooth. But developmental processes only very distantly repeat the phylogenetic facts. It certainly is inconceivable that such an organ as a tooth developed in two distinct portions that came together. Our view of the structure of the surface of living organisms requires us to believe that the enamel was deposited by the external fringe on the surface of the network on which bone was deposited. From

¹ Dr. John Cameron kindly supplied this illustration.—ED.

this point of view we may find an explanation of the marvellous teeth of the *Labyrinthodon* as due to complicated folds of the surface hardened on this same principle.

The actual appearance of the dentine is that of a hard material traversed by a network of fine canaliculi. In these lie the filaments, along which the material for the dentine travels. The outermost layer of the nodes of this network have long been recognised and have been called the "odontoblasts" as if they were the cells that produced the dentine. This substance may, in reality, be regarded as the product of the outermost layer of the protomitomic reticulum within the tooth. It is interesting to note that the canaliculi through which the "processes of the odontoblasts" or, as we should say, the "filaments of the network" run, have long been known to form a reticulum. Our theory explains, for the first time, why they should do so.

The fine structure of the tooth as a skin structure falls so accurately into line with the descriptions previously given of the various specialisations and functions of the protomitomic network, that we claim it without hesitation as confirmatory evidence.

Before concluding this chapter, there is one more point that requires emphasising. The epidermis is, in essence, the specialisation of the outer layers of the fundamental network for the purpose of making a horny covering, chiefly out of the waste matter that travels toward the periphery along the filaments. But, according to our fundamental hypothesis, the filaments are all capable of conducting nerve stimuli. Hence the fundamental filaments of the epidermis at one time also represented the peripheral nerve endings of the organism. This is a point of great importance

in view of the admitted difficulty of discovering the nerves of the epidermis, satisfactory demonstrations of which have been sought for in vain. From my point of view, I would suggest that all the filaments of the epidermis are still nervous. Whether the conveyance of thick strands of waste and other matters deadens their nervous functions or not, I do not know. It is possible that some of them do not carry streams and that these may have retained the nervous function unimpaired and thus have a special claim to be the nerves of the epidermis. It is possible also that many of the elementary sensory organs are simple arrangements for the special purpose of protecting certain groups of the filaments from being utilised by streams which would wholly or partially inhibit their nervous functions. And in this connection it is of special interest to point out that it is characteristic of elementary sensory organs to be associated with some kind of secretory activity. The streams of matter at such points do not form horn, they remain fluent, so that there is no blocking of the matter such as was described as taking place in the *stratum granulosum* (see p. 169). Whether this is the explanation of the secretory activities of the minute sense organs or not, they bear out our view in so far as they show that some modifications of the ordinary distribution of the waste matters certainly takes place when and where the nervous functions of the filaments of the fringe are required to be specially active. Some evidence as to the inhibition of the nervous functions by streams of waste matter will be found in a later chapter.

Such bundles of filaments, specially protected from streams or from being inhibited by the hardening of the streams, might give rise to tracts of fibres

running inward centrally and similarly specialised. But how far and by what arrangement stimuli received by the epidermal fringe are conveyed inward along special tracks we cannot even conjecture.

One important fact which undoubtedly has some bearing on these problems is that the dentine is sensitive, *i.e.*, that the filaments of the network depositing the bone are still capable of conveying nerve stimuli. We here have a very simple explanation of the sensitiveness of the tooth, for here again, as in the epidermis, the nerve distribution has hitherto been a standing enigma. The filaments of the network are themselves, as we shall see, nerve fibrils. In this case, again, the stimuli collected from them travel centrally along special tracks.

It may well be asked why, if the primitive nerve fibrillæ were recognised in the early seventies, so long a time has elapsed before the discovery of their destinations in the tissues? The answer to this question is somewhat curious. In the first place, a great many observations were made and recorded which showed quite clearly what became of the fibrils, but these were not accepted, not merely because their accuracy could not always be confirmed, but also because, at the flood-tide of the cell-colony theory, they were irreconcilable with it. In fact, they pointed directly to the protomitomic network which the cell-colony theory entirely obscures, and no complete answer could be given until the protomitomic network was fully recognised.

The fate of the primitive nerve fibrillæ in the tissues was the most important of the problems at which the greatest histologist of the last century, Max Schultze, was working at the time of his early death in 1874.

The evidence for its solution was already accumulating around him, for observations showing these fibrils running into nuclei were at that time increasing in number. Some observers saw the connection and others failed to see it simply because, in the former case, the fibrils were made visible by staining matters, and in the latter, not being so coated, they were invisible. In all such cases, considering the possibility of deception in so intricate a matter, a very few decided and authoritative negatives will outweigh a score of positives. Max Schultze's negative was one of the weightiest, and its result was that all observations recording the intimate connection of nerve fibrillæ with nuclei have, until now, been almost universally neglected. It does not seem to have occurred to any one that filaments could be visible at one time and invisible at another according to their physiological condition. And yet some such suggestion should certainly have been made when two observers, perhaps equally reliable, or even the same observer at different times, came to opposite conclusions as to whether fibres do or do not run to the nucleus.

In the year 1864, Frommann¹ described and figured fibrils running into the nuclei of the ganglionic cells of the spinal chord. But Max Schultze, going over the same ground, declared that all his endeavours to

¹ Virchow's *Archiv*, vol. 31, p. 134, and vol. 33, p. 168. The figures are reproduced in Kölliker's *Gewebslehre*, 5th ed., p. 252. It is true that Frommann described and figured what others had also seen and figured, the fibrils coming from the chromatin masses apparently running down the axes of tubes (*Kernröhre*). I have myself hunted for and found an appearance suggestive of these tubes. They looked like breaks or openings in the denser and more granular periphery of the nuclear networks, through which the filaments ran. They sometimes had quite irregular edges. I think there can be little doubt that these "tubes" helped to discredit the whole observation.

find Frommann's clear figure had been in vain. About the same time, Arnold¹ saw nuclear connections in the sympathetic ganglion cells, and this was confirmed by the results obtained by many others. One very interesting case is that of Courvoisier, who saw what Arnold had seen, but failed entirely to confirm his own results when studying the point again with fresh material. He then expressed his wonder that he could so clearly have seen what seemed to have no existence! The veteran Köllicker² at one time recorded two instances of processes of the nucleoli running towards a large process of the "cell" in the ganglion Gasseri of the calf, but afterwards (in the fifth edition of his work, p. 253) laid no value on the observation, for he remarked that Max Schultze, Leydig, and several other great authorities had failed to trace any of the nerve fibrils into nuclei. He admitted that such connections might exist but, if so, he asked, why are they so difficult to see? He wisely added, however, that the extreme difficulty of seeing nerve endings at all times should warn one against coming to any rash conclusions as to the falsity of observations made by such men as Harless, Lieberkuhn, Wagner, and Frommann. A very complete list of these observations is given by Retzius³ who, for reasons which are now clear to us, himself failed entirely to see any traces of nuclear connections with the nerve fibrils.

It is quite clear that the fibrils from the nucleolus or, more simply, from the nuclear network, had been seen, and everything points to the fact that the uncertainty

¹ Virchow's *Archiv*, 1879.

² Fourth ed. of the *Gewebslehre*, 1867, p. 341.

³ *Verh. Anat. Ges.*, 1889.

of their visibility was the sole reason why so many positive observations were discredited. The negative results of Max Schultze and others are now easily accounted for, and we can claim the positive observations as so much substantial evidence that the ultimate nerve fibrils can, under favourable circumstances, be seen to be continuous with the threads of the nuclear network.

But this was not all. Other evidence drawn from the central nervous system was also available. Meynert, for instance, in his classical account of the elements of the cerebral cortex, calls attention to nuclei not only angular but even running out into points which can sometimes be seen running into the processes of the "cells," *i. e.*, they can be traced into the outrunners of the cytoplasm.¹ And we may also notice the different but equally significant doctrine of Gerlach as to the fine structure of the grey matter of the spinal chord. According to this observer, the most important part of this structure consists of a dense network of exquisitely fine fibrils which he regarded as the ultimate ramifications of the processes of the ganglion cells, these so-called ganglion cells being nothing more than large nuclear nodes from which a number of reticular filaments radiate, many of which are coated for long distances with cytoplasmic matters.

Nor was evidence wanting as to the fate of the fibrillæ in the tissues other than those of the central nervous system, for Pflüger's detailed observations on the salivary glands were marvellously clear. He saw and figured the primitive nerve fibrils opening out and running as filaments into the "cells" which line and form the tubes

¹ See Strecker's *Manual of Histology*, tr. 1872, Fig. 22, p. 100.

of the gland (Fig. 30 A and B). Within these "cells," the filaments are figured and described as running up to about the level of the nuclei. It is not said that they run into the nuclei or are in any way connected with them, but, having travelled all the way in special bundles from the central nervous system, they enter

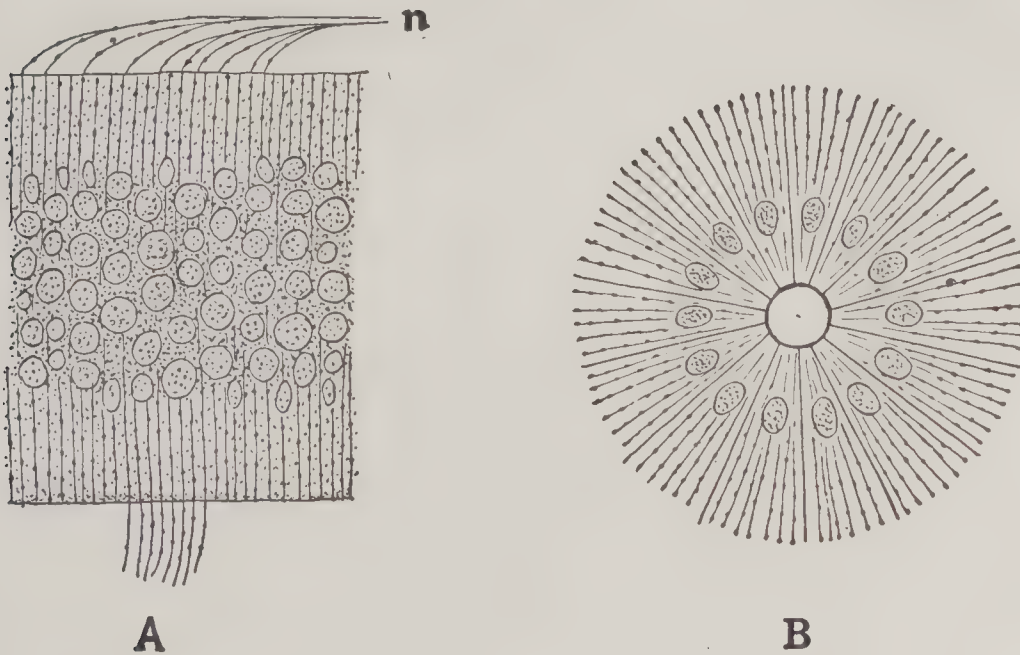


FIG. 30

Sections of a tubule of the salivary gland (after Pflüger, in Strecker's "Lehre von den Geweben"). A, an optical section showing primitive nerve fibrils expanding at *n* from an axis cylinder, penetrating the "cells" or energids which form the walls. The fibrils are all beaded with the staining matter. B, a transverse section showing the beaded threads, the primitive nerve fibrils running towards the nuclei, near which most of them are seen to end.

the cytoplasm and all run toward the nuclei; none are seen beyond the nuclei. Now, even according to the cell doctrine, the nucleus is the special organ of the cell, and the conclusion that the filaments must run to the nuclei, even though the last link in the connection was not at the time visible, is surely a very natural one, especially when taken in connection with the figures above alluded to. The sudden in-

visibility of protomitomic filaments for a short way immediately round the nucleus is, for us, quite comprehensible.

Again, several observers, Arnold, for instance, had described in detail the fibrils running to the nuclei of involuntary muscle fibres. Here the fibrils formed a network whose filaments passed through the nucleus, and the chromatin granules of the latter were suspended at its nodes. No observation of the protomitomic network could be clearer.

Lastly, Hensen has described and figured the nerve fibrils ending in the nuclei in epidermis "cells" in the Tadpole, and Professor Haycraft described and figured, with frankly expressed surprise, nerve strands ending in the nuclei of the epidermis of the Tortoise.

Here we have a large number of observations revealing the protomitomic network. The nerves, which were admittedly bundles of exquisitely fine fibrils, ran from the central nervous system to organs seen, according to these observations, to run into nuclei at both ends. Max Schultze, indeed, clearly saw that if the observations above referred to were correct, the nuclei and nucleoli would be the centres of a fibrillar system. This system, he confessed, would make it possible to explain the multipolar ganglionic cell, with its one axis cylinder process and its ramifications breaking up into the nerve plexus described by Gerlach, as a dispersal and sorting out of the nerve fibrils of the axis cylinder process so as to join filaments from the processes of other ganglionic cells, and thus to come into communication with the fibrils of other nerve strands. But, not perceiving that the linin filaments might be visible at one time and invisible at another, he remained true to the negative results of his own observations

and would go no further than this, that the nerve fibrils, after entering the "cell-body," seemed to form a felting round the nucleus, but had no direct communication with it.¹ There he let the matter drop and he did not live to take it up again. But we recognise now that the protomitomic network was very nearly discovered more than thirty years ago, and it is a significant fact that it was the study of the nervous system that almost revealed it.

I may add to the above observations that the filaments of the nerve strands have been actually seen by me both in the retina and in the nasal epithelium, running into the nuclei, and that, when examining the brains of tadpoles in the light of the experience gained from my long study of the retina, I found the same internuclear connections that I had seen in the nuclear layers of that organ (see p. 238). In very young brains, where the nuclei were crowded together and the whole choked with yolk granules, I found short connections, for the most part thickened by yellow matter (probably the substance of the pigment which forms in such abundance in the brain at that stage) and consequently quite easy to demonstrate; at a later stage, when the nuclei had moved apart, I could still make out longer connections, though they were then much more difficult to see.

¹ The reticulum of the "cell-body" is, according to our theory, continuous with that of the nucleus.

CHAPTER XI

THE CENTRAL NERVOUS SYSTEM IN THE VERTEBRATES

IN spite of the many works that have been written and are still being written on the nervous system, its origin, its constitution as a whole, the nature of its association with the organs, and the cause of its dominating character over the rest of the organism are still unexplained. Why it should be present in animals and absent in plants, in spite of the fact that there are plants that respond to stimuli, is not understood, nor have the psychic phenomena of which it seems to be the physical instrument been explained in any satisfactory manner. If any theory is brought forward that seems to throw light on one set of phenomena, it has to be condemned because all the rest retreat before it into still greater obscurity.

Now, it is just to the nervous tissue that I appeal with most confidence as establishing beyond question the truth of the protomitomic theory. Although that theory makes no claim at present to throw light upon the mysterious psychic element, it does, for the first time, afford a clear and simple solution of other problems relating to the origin, structure, distribution, and dominant character of the nervous system. It will be found, indeed, that that system falls naturally into its place in our evolutionary scheme, not as a mysterious organ added for the purpose of co-ordina-

tion, but as one present from the first, the evolution of which has gone on step by step with that of the organism itself. The evolution of the nervous system is, indeed, but another aspect of the evolution of the whole organism.

The filaments of our cell unit were, by the hypothesis, not only capable of contracting back to the chromidial centre, but also capable of conducting nerve stimuli, whatever is implied by that term. Hence, every undifferentiated linin chromatin network, built up by the multiplication of these units, was necessarily a nervous organism, each filament of which was capable of conducting nerve stimuli that would ramify through the whole length and breadth and height of the network.¹

Here we have the origin of the nervous system. *Every undifferentiated organism was an undifferentiated nervous system*, and the differentiation of the organism and that of the nervous system have gone hand in hand apparently on one constant principle, the progress being, to adopt the phraseology of Herbert Spencer, "from homogeneity to heterogeneity." The originally uniform network became differentiated by the specialisation of certain tracts for some one or other of the elementary non-nervous functions, the necessary consequence being that, in varying ways and degrees, those portions and tracts became less and less available for the conduct of nerve stimuli.

The nervous system has thus not been built up synthetically out of and within any colony of multiply-

¹ Here the suggestion arises that, as the filaments of a network could not contract completely back to any particular chromidial centre, owing to mutual restraint and to the pulling in different directions which must occur in the presence of so many chromidia, the nerve stimulus in its purely physical aspect may ultimately prove to have been, originally, merely a hindered effort at contraction.

ing cells, as proclaimed by the current doctrines, but was there from the beginning, commensurate with the organism, a continuous, though undifferentiated, whole. Its differentiation and specialisation have been twofold. In the first place, the differentiation of other tissues and organs for special functions brought the nervous system into relief, as it were; what remained, after that differentiation had taken place, ramified throughout the whole organism, retaining the primitive nervous functions intact. And, in the second place, this remainder itself underwent intrinsic specialisations which became increasingly complicated as the whole organism advanced in complexity. In this way, an organ was evolved not only as a co-ordinating instrument for the most efficient exercise of the nervous functions, but also, in its later development and *pari passu* with the rise and development of social life, for the expression and evolution of an order of psychic phenomena in intimate association with our physical life and yet so mysterious as completely to baffle our powers of imagination.

This, then, is the way in which we approach the nervous system; the rest is a matter of detail. How many of the difficulties mentioned above as having hitherto proved insoluble are cleared away by the simple origin that we are enabled to assign to the whole system will only be appreciated when the details of structure come up for discussion in the light of these principles. But before plunging into these, it is advisable to make the principles themselves perfectly clear, since several distinct propositions are involved, which, though together forming a coherent doctrine, can be treated separately and in logical sequence. All of these are important and, strange to say in relation to

such a much discussed subject, all of them are more or less new, for the simple reason that the point of view has hitherto been so very different.

(1) The first of these propositions is that every linin chromatin network and every filament of it, whether in the nodal tangles or stretching from node to node was, from the first, capable of conducting nerve stimuli which we assume must also from the first have had their psychic accompaniment of the simplest kind. We thus start with an organism which was essentially nervous; not only knit together by nervous filaments, but actually composed of such filaments *plus* other substances upon and entangled among the filaments. This supplies us, *ab initio*, with the ideal starting point authors have had to postulate in order to enable them to offer any explanation at all of the nervous system. A primitive nerve plexus has been sought for, and traces of it have been discovered in Cœlenterates and invertebrate embryos, but little has been gained by these discoveries, because the cell doctrine, with its chains of cells as the only known units of structure, supplied too coarse an instrument of analysis. The cell, so useful as a unit for tracing the general evolution of metazoan tissues in the mass, fails for the analysis of the subtlest and most pervading of all the tissues, the nervous system; for this we must have recourse to the elements of the primitive unit itself, the ultimate fibrils and the chromidial centres. Nothing coarser than Nägeli's hypothetical reticulum, built up of longitudinal rows of molecules which he called "micellæ" would suffice, and this is now revealed to us, no longer as a vague hypothesis which has to be mentally built up out of imaginary molecules, but as a structure, the existence of which can be actually demonstrated,

though its molecular constitution needs to be worked out.

(2) My next point is that the principle of differentiation of this primitive nervous system consisted of the withdrawal of portions of the network from functioning as nerves. This relinquishing of nerve functions has not been active but passive, nervous functions being interfered with and more or less completely inhibited by the fact that the filaments concerned are required for some other function for which they have to be specialised. The question of how far the specialisation of a filament for one function deprives it of its other functions is one we cannot yet decide. It is a possible suggestion that specialisation of any one of the elementary functions, with total or partial inhibition of the others, may be due to the development of special environments of the elements concerned. Whether this is correct or not, and however far this development of one function with inhibition of the others may go, we certainly have evidence, in every complex organism, of the fact that the bands specialised, say for contractility, are not primarily conductors of nerve stimuli, and that there are bundles of filaments specialised for the conduct of nerve stimuli which are not primarily contractile. But, concurrently with the specialisation of bundles of filaments for contraction and for the synthetic functions, and their consequent complete or partial withdrawal from forming part of the ultimate nervous system proper, large portions of the network itself became separated off as specific organs. This affected the nervous system in two ways; (i) the amount of the network available for the building up of the main nervous system was still further limited, and (ii) inasmuch as each specific organ enclosed a

certain portion of the whole, each had its own nerve plexus to be differentiated—a small portion of the whole yet with a specialisation of its own. Thus, step by step, the differentiation of the nervous system follows the increasing complexity of the organism; indeed, the two apparently distinct processes are only different ways of looking at one and the same process, the essential principle both in the main system and in the system of each organ being that the specialisation of tissues for any function tends more or less completely to inhibit their elementary nervous functions. Thus, although it is possible that the primitive and inherent function of the filaments is never inhibited completely and finally, but only to a certain (varying) degree, and although, further, the parts in which inhibition is most nearly total and complete are not numerous or extensive, still, for practical purposes, we will regard only those portions of the original continuous network as nervous which retain their primitive functions unimpaired by any other specialisation.

(3) My third and last point is that this residual portion of the nervous system which retains its primitive functions has itself become highly specialised, not only to be a perfect organ for co-ordinating the functions of other more or less scattered and distant organs, but also for the evolution of psychic functions which, though strictly biological in origin, are the subject of the science of psychology.

From this general statement of the fundamental principles on which the nervous system must necessarily be discussed from the point of view of our theory, we appeal for confirmation to the known facts of the distribution and structure, coarse and fine, of that system. All the lower stages, from the original un-

differentiated network upward, are obviously included in the scheme, but each of them would require to be treated in relation to the peculiar and distinct organogenesis of the group of animal forms to which it belongs, seeing that, on our theory, the development of a nervous system is only another way of describing the development of the organism. We shall have to confine ourselves here to its evolution in the Vertebrates, and shall treat of it as the residuum of the fundamental network after the other tissues and organs had been specialised.

Although the evolutionary processes went on concurrently, we may, for the sake of argument, regard the central nervous system as having arisen out of the undifferentiated remains of the original protomitotic network after all the rest of the special tissues and the organs had been separated off. The term central is often applied merely to the greater masses of the brain and spinal chord, but I mean here all that part which does not belong to, or is not included in any of the specific organs within each of which the network has developed a subsidiary nervous system of its own. We have now to ascertain whether the central system of the Vertebrates does or does not, in fact, accord with this description.

Organ formation appears to have commenced internally by the development of a digestive cavity, for the feeding of which peripheral organs would arise: organs of sense, organs for the prehension of food and, in addition to these, peripheral organs for locomotion and for defence; then internal organs would develop: reproductive organs, and others accessory to reproduction, and again organs accessory to digestion would arise between the digestive canal and the peripheral organs. Now, if we try to picture to ourselves the residual network that would be left between these

organs as they arise out of the continuous network, we see at once that it must form a plexus. Masses of various sizes would remain, joined together by strands of varying length, and the whole would necessarily encircle the central alimentary canal. Since, again, the Vertebrate is bilaterally symmetrical and has a dorsal and a ventral surface, and since the development of organs takes place chiefly at the sides of and below the alimentary canal, we ought to find the largest undifferentiated mass on the dorsal side of the canal and a number of smaller masses laterally and ventrally. Now this is exactly what we do find. Dorsally, we have the mass afterwards specialised into the spinal chord; on each side of this we have the separate masses known as the spinal ganglia; while, ventrally, we have the rows of sympathetic ganglia, all these masses being connected together by thicker or thinner strands into a continuous plexus. These condensed masses of the original network still persist, joined by strands, all the masses and the strands doubtless somewhat altered secondarily in shape, position and size, but all bearing unmistakable evidence to the correctness of our view as to their origin. It may be true that it is not easy now to assign them all their exact places, *i.e.*, to say exactly between what organs they arose, for the vertebrate body has undergone considerable modification during its evolution, always in the direction of concentration and localisation of special functions; organs, which at one time arose as a series of smaller organs have, in process of time, coalesced to form large compact masses.¹

¹There are, indeed, sufficient traces of the serial formation of organs in the past to justify the belief, that the vertebrate body passed at one time through a stage at which it was segmented like that of a true or segmented worm.

Of the principal specialisations of this primitive residual plexus, I may mention first the enormous secondary development of the anterior end of the great dorsal mass. This can be analysed into several swellings succeeding one another and ending in the great cerebral lobes which, in Man, cover the rest like a large cap. In the human brain we thus have a striking example of secondary growth as one of the possible causes of differentiation.

The next specialisation of interest to us is that of the older and longer nerves running out to the peripheral organs (and consequently liable to torsion and stresses), which become protected and isolated by special sheaths. These latter must be referred, like the nerves themselves, to a special arrangement of drawn-out portions of the original network. The innermost portion of such a strand came to contain the filaments conducting the stimuli, and these were protected by a special arrangement of the outermost layer of the strand.

In contrast with these older, longer, and consequently more specialised strands are many newer and shorter strands which seem to have arisen in connection with purely internal organs, and which show no such arrangements for isolation. We find these strands, indeed, not differing much from what we may imagine that the protomitomic network would have been like had its filaments been gathered into strands and then drawn out. Such naked, sheathless fibres are specially numerous in the sympathetic nervous system, where they sometimes still run as reticulated web-like bands stretching freely among the tissues. These nerves have large nuclei scattered along their courses or gathered into clumps at nodal points. They might, as I say,

be regarded as stretched portions of the original network with perhaps their nuclear nodes specialised in various ways in accordance with the nerve functions required of their filaments.

But while this description of the general plan and arrangement of the central nervous system shows that it may well have arisen as a plexus of residual masses and strands of the original network left when the specialised tissues and organs were separated off, it is only when we come to study the minute structure that we find that it must have been so. As soon as we look below the surface, we find once more the elementary linin filaments and the chromidia which, as has already been shown, are the ultimate structural factors for the analysis of protoplasm. Here and there, it is true, they are grouped into typical "cells," but these are themselves elaborate organs in the nervous system, not the units of its structure. Of these two, the filaments and the chromidia, we should expect that, in a system like the one we are now dealing with, whose chief function is the conducting of stimuli, the former would be the more prominent, and naturally the filaments are the elements we have most interest in demonstrating. We know little about the actual function of the chromidia, except that they are necessary to the vitality of the filaments, and what we shall have to say about them will be largely in the way of suggestion.

With regard to the filaments, I recall the well-known fact that the one essential element of structure of all nerve strands medullated or non-medullated, *i.e.*, from our point of view, with or without sheaths, is the primitive nerve fibril. Every nerve strand is, in essence, a bundle of such fibrils, and we are therefore

justified in concluding that these fibrils must be the conducting elements. So delicate are they and so difficult to see that it was long before histologists were agreed even as to their existence. They have now, however, been demonstrated beyond doubt and the significance of their presence for our argument cannot be overestimated. For, if the fibres of the protomitotic reticulum which, according to our theory, are capable of conducting stimuli, were collected, as we have assumed that they were, into bundles, they would have been as fine and as difficult to see as these primitive nerve fibrillæ. That these strands should consist of bundles of the primitive fibrillæ, whether they are provided with protective sheaths or not, is clearly accounted for by our theory. No such bundles of strands would be needed unless distinct organs developed. The stimuli from one part of the undifferentiated reticulum can find their way along any of the filaments to any other part. It is only when a portion of the underlying reticulum has been more or less detached as an organ, and yet remains in organic connection with the rest by specialised bands and bundles of filaments, that certain strands, consisting of undifferentiated linen filaments, are required for the purpose of conveying the stimuli from the organ to the rest of the undifferentiated network from which it has been partially separated.

In the early stages of organ formation, we have to imagine the filaments of the network of the organ collecting together at its proximal surface into a bundle, in a way with which the figures of, for instance, primitive eyes have familiarised us and, further, we must picture to ourselves this bundle opening out after running across the space which separates the organ from

the central nerve mass, and dispersing again into the network of the nerve mass. Apart, then, from any theory of the origin and morphology of the nervous system, we may describe it as so many specialised bundles of elementary filaments which open out proximally into the central mass and distally into the masses of the organs or tissues, and it is enough if we now consider the matter from this bald point of view.

First let us turn our attention to the central nerve mass into which all these bundles of filaments open and disperse and run into one another, for the co-ordination and transmission of stimuli. When we remember all the possibilities of secondary growth of organs and tissues, with consequent multiplication of nerve fibrillæ, we should say, theoretically, that the central mass could be little else than a confused plexus of these ultimate filaments. This is exactly what we find. For if we strip the nerve chord of all the specialised bundles which are now involved in its mass before opening out, and confine our attention only to its central and essential part, into which they do open out, viz., to what is known as the grey matter, we find that this does appear to consist of a close tangle of the finest filaments. It is called in German the "Punksubstanz" for, in section, it appears as a mass of the finest dots in a kind of haze. I am inclined to believe that this tangle of filaments is held in place, so that the filaments themselves do not touch, nor run together indiscriminately, but only according to the required order, by means of a subtle cytoplasmic framework which they themselves build up, just as they build up frameworks and pellicles. There is no difficulty in this supposition; all we require to imagine is that, in a close, generally diffused tangle, the nerve

stimuli pass easily along certain definite paths, but that they are more or less inhibited by the presence of other matters from passing along other paths, and these others would constitute a framework. Or, again, the framework may be thought of as purely cytoplasmic, *i.e.*, as membranes built up by the synthetic action of the filaments but not necessarily with any close frame-work of filaments underlying them (*cf.* Chap. XII on the membranes forming the rod vesicles of the retina).

Whatever be the origin of this supporting framework, we gather that our main argument is correct from the fact that, in the lowest Vertebrates, such as *Amphioxus*, in which there is no pronounced organ formation and in which the spinal chord is not complicated by numbers of specialised bundles, the whole of the central mass consists, except for its nuclei or energids, exclusively of this "Punksubstanz." But it may be remarked that, according to the protomitomic theory, the filaments, on dispersing from their specialised bundles ought, sooner or later, to find their way to the nuclear nodes. It is quite possible that individual filaments might first lose themselves in the tangle above mentioned, but certainly the nuclei ought to be seen to be in filamentous connection with the filaments of that tangle.

And this brings us to the functions of the nuclei which, in the great ganglion "cells," are clearly very important organs.

Hitherto, while not losing sight of the chromatin as the inseparable accompaniment of the linin network, we have been chiefly occupied with the latter. This has been natural enough considering that we have been discussing the forms of life and of living tissues, and

that these depend wholly upon variations in the shape and arrangement of the network. We now propose to focus our attention more especially on the physiological element of the network, the chromatin, and on some of the phenomena associated with it, prefacing our special argument with a short retrospect.

The chromatin first appeared in our hypothetical unit as a central chromidium. This grew and, on reaching a certain size, divided into two. Each chromidium is found, characteristically, at a centre where several linin threads meet. When a chromidium divides, the threads or some of them, at least, also divide. The reasons for this cannot be given, nor can we answer the question whether the chromatin divides the threads or the threads the chromatin. We seem driven to conclude that there must be some definite constitution about the chromidia, because of their universality in all protoplasm: not only are they found scattered over the networks, but combined in masses so as to form large chromosomes. It is known that masses of chromatin, however large, may break up into clouds of minute bodies, and we may perhaps assume that these large masses of chromatin are chromidia bound together on a close network; that they are always associated with the linin filaments we gather from the fact that, when they disperse, it seems always to be along the filaments of the network. It is possible that, when massed together, they are all embedded in some other substance which acts as a matrix, either nutritive or composed of waste that is being got rid of. It is perhaps these matters which, thrown off during division, stream away along the filaments and make the latter visible, revealing them suddenly in their division figures.

It is known that the chromatin is used up and disappears in starving organisms and that it increases in amount in those that are well fed. When we compare the size of the masses of chromatin in a protoplast with the extreme tenuity of the filaments, and remember that the filament is comparatively stable whereas the chromatin is used up in the vital processes, we may conclude that a large food supply must be needed for the replenishing of the chromatin, so far, at least, as it is converted into the substance of the organism. The larger part of it serves as material for building up the more solid frameworks which have rendered the development of large complicated organisms possible. That chromatin masses containing nuclei are not always in the same chemical condition has long been known, nor have they always the same microscopic appearance.

How far the linin itself is a form of chromatin we have no means of knowing. The belief is frequently expressed that the two are closely akin, but this belief seems to be largely based upon the fact that the threads which appear during the process of division take stain. These, however, do not represent the true filaments but, undoubtedly, matter that has been in close association with chromatin disposed upon the filaments. I am inclined to regard the two substances, linin and chromatin, as entirely different and to believe that the phenomena of life are due to their association. The filaments may perhaps continually rob the chromatin of molecules which have to be replenished. But here we are dipping down into the unknown, for the real nature of growth, of contraction, and of the physical aspects of nerve stimuli can be a subject of speculation only. Even all speculation fails

us when we come to the psychic phenomena which are known to accompany some of them and which, we naturally conclude, accompany them all.

We have already shown how inseparable the filaments and the chromatin are: how the chromatin travels upon the filaments, shrinking together under sudden stimulus, but spreading out in all directions wherever needed for the production of vital energy, or for taking part in some constructive processes, such as the making of any secretions or excretions; experiments have shown that it is necessary to life. When protoplasts are cut up, the portions which contain chromatin can live so long as the chromatin lasts; without it they die. Those that contain the nucleus can regenerate the missing parts. The chromatin always appears to move along the filaments; these are the rails along which it travels from the centre outward. This is the case not only in the protoplast but in every energid of a metaplast. The chromatin comes from the nuclear centre and is used up in producing the energies of the filaments. Now the question arises whether, since the whole organism (say of a Vertebrate) is of a higher order than either the chromidial unit or the protoplast or "cell," and, since in each of these we have the central stores of chromatin which, as we have seen, are drawn upon by the surrounding network for its responses to the environment, the same rule does not hold in the case of the highest metaplast. Does not the great residual mass of the network, after the organs and the tissues have been separated off, function as a nerve centre for the co-ordination of the vital processes of the organism? When we come to analyse this great nerve mass, we find it to be, on the one hand, a maze of threads running in all directions, uniting the whole into a single organ-

ism and, on the other, a vast storehouse of nuclei. The central nervous system, with its great stores of ganglionic nuclei, may, I believe, be regarded as the analogue, in the entire organism, of the nucleus of the protoplast, answering as it does fairly well to the description given of the nucleus in the foregoing pages, viz., that it is a special tangle of the reticulum from which the filaments of the network radiate outward in all directions and in which the chromatin is stored.

Let us follow this parallel¹ out more in detail, considering the central nervous system (1) as a central organ for the storing and perhaps for the manufacture of chromatin and (2) as a centre for the co-ordinating of the responses of the organism to stimuli.

I. The central nervous system may be roughly described as consisting of three elements: (1) great strands of nerves departing to all parts of the body; (2) fine molecular substance into which the fibrils of these nerve bundles open out; and (3) masses of nuclei or "nerve cells," as they are called. These latter may again be roughly divided, as in the retina, into smaller nuclei with little or no granular cytoplasm around them, and larger nuclei with considerable aggregations of this matter, the nucleus, with its cytoplasm, being what is called a "ganglionic cell." It is these countless thousands of nuclei which now attract our attention, each with its store of chromatin; it is they that justify us in regarding the brain and spinal chord as essentially a vast storehouse of nuclei each of which has its own store of chromatin. There is some reason, as we shall presently see, for believing

¹ That this parallel is more than a mere fancy is made probable by the ascending series of units to be traced in Part II.

that chromatin is being actively manufactured and distributed by the great ganglionic cells.

II. Passing to the second point, that from this storehouse the chromatin is distributed to the rest of the body, the nerves and filaments acting as lines of distribution, I would suggest that, however improbable this may sound from the point of view of the cell doctrine, it is directly deducible from the fundamental proposition of the protomitomic theory. I have shown that, in some of the Protozoa, the primitive protomitomic reticulum seems to have had what is called a diffused nucleus, *i.e.*, that the chromatin was scattered about over the network and the activities of the different parts depended upon their local supplies. At a later stage, the chromatin, in the interest of organic efficiency became localised in a central nucleus and an even supply was sent along the filaments to the different parts according to their needs. We are justified in assuming that any such fundamentally important physiological process as this distribution of chromatin from the central store to the periphery, found in the protoplast, would persist in all later complications of the protoplast and the metaplast, remaining, indeed, as one of the elementary life-processes as long as there is any life on the planet. The chief difference between a protoplast and an organism like the human body, besides the greater size of the latter, is its specialisation into a complex of organs grouped round a condensed residual portion which functions as a co-ordinating centre to which all the rest are attached. This specialisation has apparently entailed a gradual enormous multiplication of nuclear centres, not only in the different organs, but in the residual nervous system.

The streaming of chromatin along the protomitomic

filaments, which has been shown to take place always from the central nucleus to the periphery, both in the protoplast and in the energid, has now to be discussed

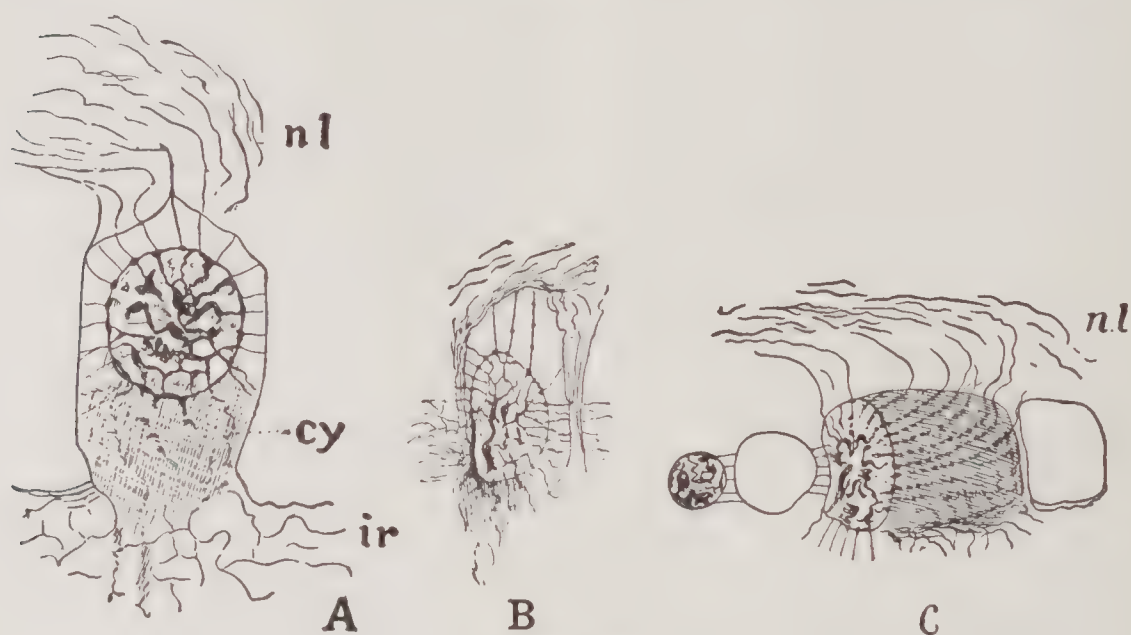


FIG. 31

A, B, C, D, E, Ganglionic cells from the Retina.

- A. The cytoplasm is here massed on the distal side of the nucleus; there is none on the proximal side. The filaments running distally from the nucleus are obscured by the cytoplasm (cy) excepting in so far as they are coated with chromatin. (ir) inner reticular layer. The fibrils of the nerves are seen to bend down, to run through the syncytial membrane and to enter the nucleus.
- B. A ganglionic nucleus from the retina of a Plaice, with granular cytoplasm streaming from one side, and with the threads of the intranuclear network radiating outward, some of them going to the nerves with beads upon them.
- C. Several of the nuclear filaments running to the nerves pass through the granular cytoplasm and are visible because dotted with beads. Near the edge of the cytoplasm the beads become large, shapeless clumps. Note the contrast between the thick staining primitive nerve fibrillæ and the connecting filaments.

in the light of our conclusion that the protomitomic network is, in its entirety, the nervous system. We shall bring what evidence we can to show that chromatin passes through a tissue from nucleus to nucleus and that it may come to that tissue along the primitive

nerve fibrils opening into it. This can be best illustrated from the retina (Fig. 31, A, B, C, D, E), where I found that the chromatin stored up in the rod nuclei travels outward along the protomitotic filaments to be used up in the functional activities of the rods. That

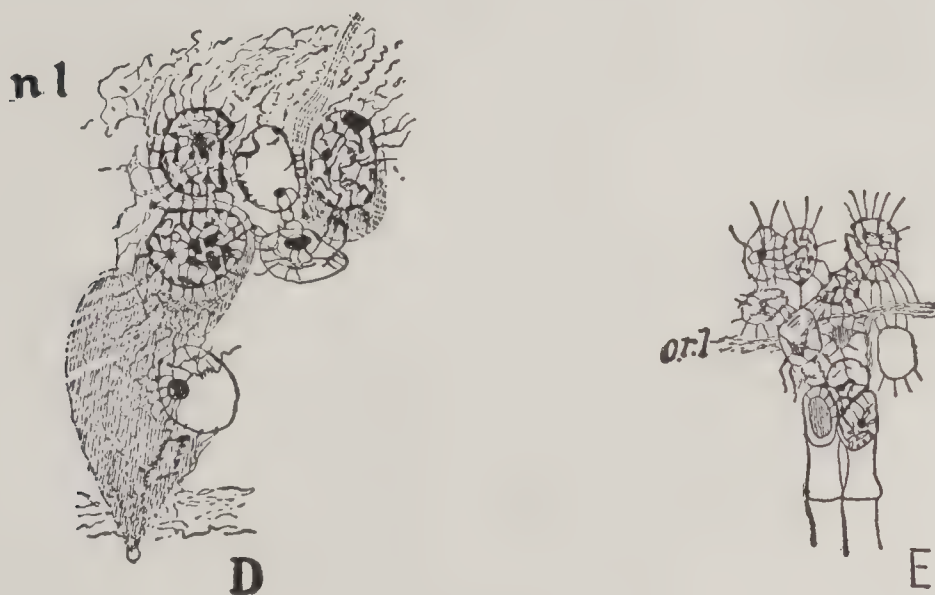


FIG. 31

D. A group of ganglionic nuclei joined together by filaments which are continuations of the intra-nuclear networks; proximally the filaments run into the fibrils of the nerve layer nl which are shown cut either across or slightly obliquely. Three of the nuclei have granular cytoplasm on their distal sides. The Nissl's Schollen are seen very closely associated with the nuclear filaments, and then appear comparable with such masses of extra-nuclear chromatin as are shown in Fig. 35 A.

E. Nuclei of the middle and outermost layers not only connected *inter se*, but the nuclei of the one layer with those of the other through the outer reticular layer (Amphibian).

chromatin disappeared from the rod nuclei of the retina after the latter had been exposed to light had been previously shown by Gustav Mann.¹ But that author made no suggestion as to what became of it,

¹ *Journ. Anat. and Phys.*, 1893, p. 100; in the case of nerve cells generally the author found that, in rest, the nerve cell stored up chromatin which was used up during activity.

i.e., as to how and in what form it left the nuclei. The protomitotic reticulum, as shown in the retina, answers both these questions. In the first place it is found in quantities outside the nuclei on all the filaments of the rods, and all the microscopic appearances lead us to conclude that it escapes along the filaments from the rod nuclei. These, however, unaided, could not supply enough even for the initial formation of the rods, still less for maintaining them in functional activity throughout life. The microscope, however, showed us the chromatin clotted together on the tangle of the protomitotic filaments joining the rod nuclei with those of the middle layer, from which it could be seen escaping outward. The chromatin could be traced through the outer reticular layer and into the rod nuclei. And, lastly, the supply in this middle layer seemed to be traceable to the "Nissl's Schollen" of the so-called "ganglionic cells" which are clouds of minute granules of chromatin derived from the nuclei, and which can be traced into streams running outward down the cytoplasmic processes of these cells or, as we should describe it, along the protomitotic filaments, coated over with the cytoplasmic matter which forms these processes (Fig. 31, D). That the "Nissl's Schollen" of ganglionic cells in general are used up during activity was also one of the results obtained by Gustav Mann.

Here, then, we have the chromatin passing outward through a complicated tissue from nucleus to nucleus. We may compare it and at the same time contrast it with the streaming matter described in the epidermis, where the chromatin seemed to be drawn away gradually from the epidermal nuclei, leaving them empty

shells before final transformation into horny plates. There are no such continuous and, except for the occasional appearance of pigment granules, uniform streams here. On longer filaments, the chromatin mostly occurs in minute beads or "varicosities" (Fig. 31, C), as older authors would have styled them, but thin continuous streams also occur. On the network of filaments running from nucleus to nucleus, it may appear in large shapeless clots (see Fig. 35, F, p. 224). It is, of course, possible that both beads and clots may be due to the action of chemicals, the continuous streams breaking up under the stimulus of the fixing agent.¹ A long, thin continuous stream might well break up into beads or varicosities while the streams were in a reticular tangle, the matter clotting at the nodes where the streams were thus entangled. Through the dense molecular layer the chromatin passes as so many minute chromidia derived from "Nissl's Schollen" which, again, are clouds of microsomes. But whether the chromatin travels in beads or in thin streams or in different arrangements of microsomes is not a matter of vital importance at present. The fact that it does thus travel through tissues and is used up is what now concerns us. For, if the migration of chromatin outward towards the peripheral nerve endings seen in such an organ as the retina, is a universal phenomenon, as I assume it to be, we are at once confronted with the problem, What is its source?

¹ My experience of running an osmic acid mixture under a cover glass in order to fix a living nucleus leads me to think that the chromatin which, in the living condition, was like a close tangle of thick threads, may break up into beads of different sizes as a result of the action of this reagent; see also above p. 49.

Two answers occur to me, both of which seem to be supported by some evidence.

(1) The retinal ganglionic nuclei may manufacture it *in situ* out of the cytoplasmic matter which is so frequently seen aggregated around them; or (2) they may receive their supply of chromatin along the primitive nerve fibrils of the optic nerve.

I do not see how we can escape from the conclusion that the ganglionic cells, not only in the retina, but wherever they occur in the nervous system, are manufacturing chromatin. They all show the same characteristics (see Fig. 31, A-E, pp. 206, 207): an immense supply of cytoplasmic matter aggregated round the nuclei, and clouds of chromidia perpetually emerging from within the nuclei and forming staining masses. That these Nissl's clumps originate from the nucleus is supported by the fact that they may be found arranged concentrically round that body. In thus streaming out from the nucleus they recall the lecithoblasts or the minute staining bodies which form the yolk and also emerge in dense clouds from the nucleus. In these "ganglionic cells," however, the discharged chromidia are not required to perform any function on the spot, but they travel away along the nerve strands to some distant place of functional activity. In the retina, they find their way through the molecular or reticular layer and on through the nuclei of the middle and outer layers into the rods.

This answer as to the manufacture of chromatin in the ganglionic nuclei with their "Nissl's Schollen" also confirms the second answer. For, if the ganglionic cells in other parts of the nervous system are manufacturing chromatin, it can only be to send it along the nerves. Hence we are disposed to assume that the

optic nerve actually brings chromatin into the retina along the primitive nerve fibrils.

This sounds startling; not only, however, does the protomitomic theory seem to demand it, but direct evidence is afforded by the beads of chromatin seen on the fibrils which run from the nerves to the ganglionic nuclei in the retina (see Fig. 31, B and D, pp. 206, 207), and also by the deep staining and apparent thickness of the nerve seen in the nerve strands as compared with the delicate hyaline filaments which join it to the nucleus. This seems to indicate that, within the framework of the nerve strand, the protomitomic filaments are covered with a stream of chromatin travelling outward, but that, between the strand and the nucleus, that stream has run together into beads.

Further, it is very significant that similar beads or "varicosities" of staining matter have long been known to be characteristic of the filaments of nerves where they open out into a tissue—say into the olfactory epithelium, and also where they run into the walls of the salivary glands (see Fig. 30, p. 185), or again into a muscle, and we may well believe that in both these last cases large quantities of chromatin are required for efficiency, in the muscles for contraction and in the salivary glands for the manufacture of the juices.

If this is the correct interpretation of the varicosities, we should have to imagine that the filaments composing the axis cylinder of every actually functioning nerve must be carrying fine streams of chromatin outward towards the periphery, streams which perhaps break up into beads under the action of the reagents. We have clear evidence of the presence of beads upon the filaments of the axis cylinder while still *in situ*, in all

the figures published of such axis cylinders and again in the Ranvier's nodes.¹ (Fig. 32).

Light seems to be thrown also on another phenomenon. When a nerve is cut across, a number of nuclei appear in the axis cylinder, and the origin of these nuclei has never been satisfactorily traced. This discussion has suggested to me that they may be due

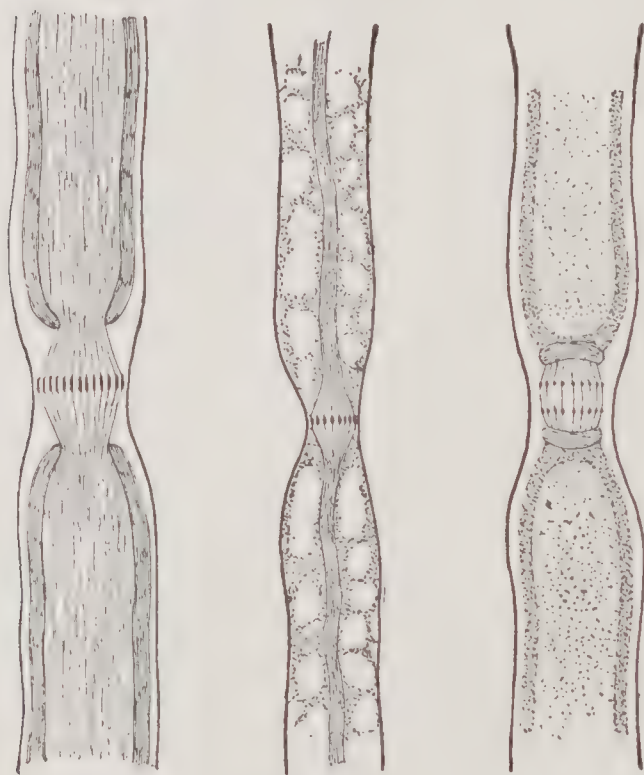


FIG. 32

Nodes of Ranvier. (Frog and Pigeon).

to tangles of the cut ends of the nerve fibrils in which the chromatin, continuing to stream out, is unable to get beyond the line of the lesion and consequently accumulates.

I may also mention the fact that the ganglionic cells are known to show signs of great shrinkage with loss of their clouds of

chromidia after severe nerve strain.

In these facts, we certainly have some evidence to warrant us in believing that the central nervous system acts both as a storehouse and as a manufactory of the chromatin, which travels away along the fibres and bundles of fibres of the nerves to the periphery just as, in the uninucleated protoplast, the chromatin travelled along the filaments from the nucleus to

¹ The Ranvier's nodes may possibly be regarded as modified nuclei, *i.e.*, as possible storehouses of chromatin.

the regions of functional activity at the surface or elsewhere.

And here I may add, that signs are not wanting that, in this movement of chromatin to the periphery, the nuclei themselves may perhaps take part, not only by discharging chromidia and larger masses but by actually themselves migrating. A striking local migration of nuclei within the developing retina has been described by me.¹ Even the ganglionic cells of the retina can, during life, be seen to pass outward through the reticular layer until, in old eyes, the ganglionic cell layer may be empty, having lost all its nuclei, apparently in this way. Further, very minute nuclei can frequently be seen entangled among the nerve strands on the inner surface of the retina, and their appearance at times is very suggestive of their having just arrived. Lastly, it has often been stated that the nuclei in the cerebellum of very old persons may be reduced twenty-five per cent. in number.

There is therefore no doubt that active migrations of nuclei do occur, though to what extent we do not know; also that there is a using up and total disappearance of nuclei, though it is not necessary to believe that a nucleus that disappears has migrated; its tangle might perhaps straighten out, and its chromatin be scattered. A phenomenon, not exactly of this kind but suggestive of this, has been described by me elsewhere and was referred to above.

It may be that the active migration of whole nuclei from the central organ to the periphery is nothing more than a persistent trace of that primitive migration of nuclei to the surface internal or external, which takes

¹ "Studies in Retina," *Quart. Journ. Micro. Soc.*, vol. 46, pt. iii., p. 25.

place in the early metaplasts (Chap. IX, pp. 131-137), a migration to which we traced the formation of epithelia. We may regard the normal method of distributing chromatin in highly organised forms as that already described. The chromatin travels from the centre to the periphery in the form of thin streams of chromidia along the bundles of primitive fibrils which compose the nerves. It is true that long distances have to be travelled but, in a large organism, this must always be the case and in this alone there need be no difficulty. The real difficulty lies in the general conception of materials moving from place to place through the body; we have seen, however, that this is a necessary assumption of our theory; that all the materials essential to the synthetic energies of the organism in the formation of skeletons are conveyed along the filaments and, when they have reached their destination, remain massed upon these. The chromatin is closely allied with the filaments in the production of all the vital processes, and there is no reason why it also should not be distributed by means of the filaments. One of the chief and certainly one of the most mysterious of the vital processes is the functioning of the nerves themselves, and it seems to me that there can be only one answer to the question "is this perpetual streaming of chromatin along the fibrils of the nerves in any way associated with nerve stimuli or is it purely an incident in the mechanism of the distribution of material?" That there is some intimate and essential association between the streaming material and the energy of nerve stimulus is, to say the least, highly probable.

Whether these doctrines will throw any light on the more subtle disorders of the nervous system is a

question within the special province of the neurologist, but I may legitimately make one suggestion. Growth is one of the elementary activities of the filaments of the protomitomic network, and it would seem that morbid growths may be due to irregularities in the way of excessive local supplies of chromatin, excessive purely as such, or excessive because the normal supply is not properly used up. It is significant that cancerous growths, which are characterised by an immense multiplication of nuclei, with specially rich supply of chromatin, are invariably found at the free surfaces of the body or of its internal passages. For it is to these free surfaces that the chromatin is always flowing and, if not used up in normal function, it might quite conceivably cause an abnormal growth.

One strong argument in favour of this view of the causes of cancerous growth, is that the proliferation is always that of the tissue in which the growth starts. If a cancer grows in the rectum, it shows great proliferation of the tissue characteristic of the lining of the rectum; if it starts in the ordinary surface epidermis, the cancerous tissue is that characteristic of the epidermis. This is exactly what we should expect if the phenomena were due to a continued growth started by irregularities in the flow of chromatin along a special nerve or group of protomitomic filaments.

It is obvious that the correctness of this view might be tested by extended enquiry as to how far cancerous growths in their earliest appearances coincide with the areas of distribution of the nerve endings.¹ It would

¹ Mr. Cheate (*British Medical Journ.*, Dec. 12, 1903) gives several instances in which cancerous growths exhibit traces not only of being partially confined to areas of surface distribution of special nerves, but of their progress being arrested where lesions of the nerves have taken place.

have to be borne in mind that, as the protomitomic reticulum is a continuum, and the nerves probably possess only functional and not structural isolation, any excess of chromatin arriving along a nerve might easily spread out beyond the area functionally supplied by that nerve.

Conversely, certain neurotic and perhaps, also, paralytic phenomena may be due to inhibition of the flow of the chromatin. Gout may be due to partial stagnations in the flow. Gouty deposits have been found to be largely composed of nuclein, usually said to be derived from "broken down cells." These terms have now no clear meaning for us. But the deposition upon the protomitomic filaments of nuclein mixed with other substances might be expected to be a danger natural to an organism described according to the protomitomic theory.

This side of the subject, however, must be investigated by the pathologist. I write purely as a biologist, and have only ventured to touch upon this matter because all pathological phenomena are ultimately biological, and because pathological problems may well be among those on which the protomitomic theory will throw new light.

CHAPTER XII

THE SENSORY ORGANS AND THEIR WITNESS TO THE PROTOMITOMIC NETWORK

IN turning to the sensory organs to see what evidence they afford of the underlying protomitomic network, I shall take the retina first and deal much more fully with it than with any other organ, since the comparative study of vertebrate retinas has occupied me for many years, and it was this study that yielded me the first traces of the fundamental network. The network of the retina, we shall find, throws light upon several important and interesting points.

Led astray by too literal an interpretation of the shortened up processes of ontogeny, zoologists have tried to deduce the eyes of Vertebrates from the brain,¹ but there can, I think, be little doubt that all the sensory organs must be deduced from the original surface of the underlying network and its fringe. Though there may still be some doubt about the retina, there

¹ It seems to me that my view of the morphology of the brain and central nervous system as the residuum of the network, after all the portions destined for other organs and tissues have been abstracted, throws new light upon the ontogenetic origin of the retina. The brain is not a mass of independent cells which give up of their number to form a retina. It is merely a part of the whole reticulum from which one organ, the retina, has still to be separated. It is the interpretation of ontogenetic processes in terms of separate cells that has been the misleading element.

can be none in the case of the nasal epithelium and the auditory organs, the free peripheral sensory fringe

supplying us with ideal factors for the elements of these organs.

Whatever its exact phylogenetic origin, the retina is one of the most instructive organs for our present purpose, not only because it reveals the protomitomic network with special clearness, but also because being, as it were, complete in itself as an organ, it can tell us many important facts about its finer structure and physiology. The following account of the retina will therefore be somewhat detailed, in order to show how many of its most intricate problems can be elucidated by our theory.

Described in terms of "cells," the retina is

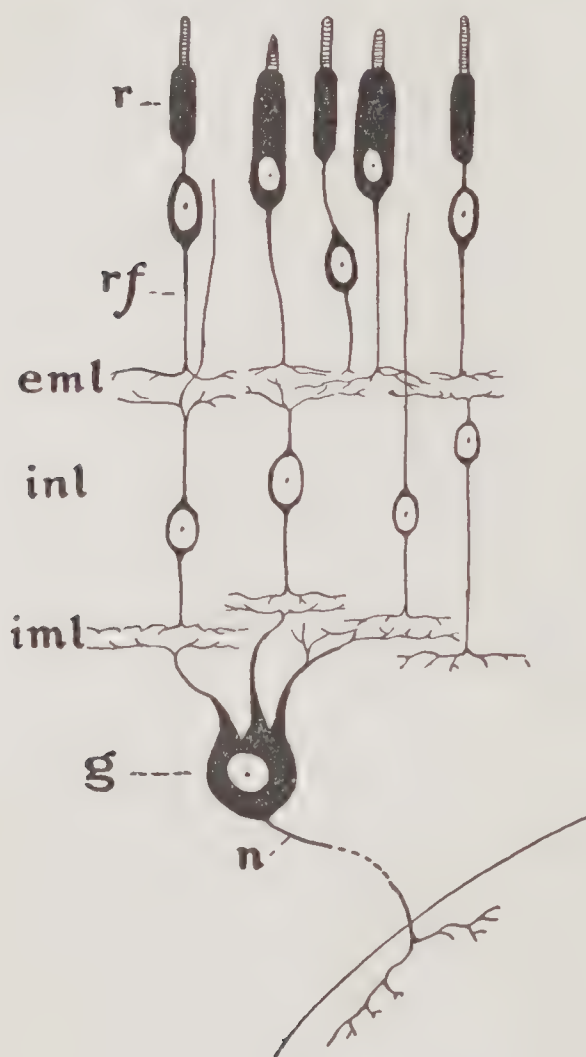


FIG. 33

Diagram showing the visual elements in the vertebrate eye. r, rods; rf, rod-fibre; eml, external molecular layer; inl, inner nuclear layer; iml, inner molecular layer; g, ganglion cell; n, an axis cylinder of one of the fibres of the optic nerve.

said to consist of five layers: three layers of cells separated by two layers of some fine matted tissue. The diagram Fig. 33 shows the surface of the cup covered with a smooth, dense layer of very fine, hair-like projections, the rods (r); these are the special cell-structures

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which are stimulated by the light, and what they "feel" is conveyed, presumably from "cell" to "cell," through the retina to the nerves (n) which are spread out over the inside of the cup.

The innermost layer of cells is said to consist of a row of large "multipolar ganglionic cells" and what this means is shown in the accompanying diagram. They are cells which send out thick cytoplasmic processes in various directions, one of which from each "cell" is *said to be continuous with a nerve fibre*. The remaining processes, one or all, it is assumed, collect the stimuli from the rods, and transmit them through the cell and along the aforesaid nervous processes to the brain.

The second layer is the thicker of the two zones of matted tissue which intervene between the rows of "cells." In it the distal processes of the "multipolar cells" just described are lost sight of. It has always been a puzzle how to account for this matted layer on the cell theory, for no cells can be found distinctly and certainly to belong to it, although, according to the cell doctrine, every part of the body must have been built up of or by cells. No one has succeeded in demonstrating such formative cells either for this tissue, or for the outer reticular layer, which is much thinner than the inner.¹

The cells of the next or middle layer, which is also the thickest of the three cell layers, were evidently more puzzling to the early anatomists than the ganglionic cells, for they do not look like orthodox cells. They are not masses of protoplasm each containing a nucleus.

¹ It is obvious that such layers are easily explicable according to the protomitotic theory, the fundamental continuous network being the one essential underlying structure.

All that can, as a rule, be seen is so many nuclei, and they were consequently first called "granules" (Körner) by German writers. As it was impossible, according to the cell theory, that they should be nuclei alone without any cytoplasm, a cytoplasmic envelope was assumed for them and they are always figured as if suspended in spindle-shaped strands arranged radially (see the diagram). On the assumption that they must also be nervous and carry forward the stimuli on their way from the rods to the nerves, they have been called "bipolar ganglionic cells," that is nerve "cells" with two processes, to distinguish them from the multipolar cells of the innermost layer.

After this layer of supposed spindle-shaped "cells" comes the thin, outer, intervening layer of matted tissue already referred to, and then the outermost layer of cells called, because the rods appear to belong to them, the "visual cells" (Sehzellen). The form of the visual cells is of special interest. They are described as greatly lengthened out, one part, which contains the nucleus, remaining in the body of the retina to form the layer of hair-like processes (rods) above mentioned. The actual structure of these rods has been matter of speculation; they were said to be refractive and to consist of some substance allied to the horny matter of the skin. Fine fibrils could be seen running down them, at least near where they join the retina.

The cell doctrine of the retina teaches that the rods are "individuals" specially modified for the reception of light stimuli which they hand on, perhaps along the fibrils just mentioned, to the two inner rows of cells which are also "individuals" specially modified for the transmission of these stimuli from layer to layer and so into the nerve and to the brain.

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This, until recent years, was the cellular account of the retina. It not only, as we see, failed to elucidate the origin of the two reticular layers, but also failed to account for the conveyance of the stimuli from the visual cells through the retina to the nerve layer, for neither of the two matted layers nor the middle cell layer suggested any structure specially adapted for that purpose. On the one hand, we have the nerves running in bundles of filaments and, on the other, rods as the special instruments of sensation packed together regularly; one would expect to find that the connecting strands between these two would be equally regularly arranged as fine parallel striæ, but no such regular connections exist.

The passage of the stimuli from the rods to the nerves became, therefore, under the cell doctrine, the great problem of the retina. Max Schultze, who had discovered the faint striæ above mentioned on the rods, claimed to see others again in the "rod-fibres" (see Fig. 33 rf). But there were not enough to bridge over the gap.

At this unsatisfactory stage the problem stood until some twelve years back, when a new method of research brought hope. The metal impregnation methods elaborated by Golgi were found capable of demonstrating what were thought to be the finest ramifications of "cells." The startling results obtained by applying them to the retina gave rise to an entirely new doctrine of nerve origin and connection, the neurone theory. No direct connection was discovered between the "cells" of the retina which partly fill in the gap between rods and nerves. These "cells" were found to preserve their individuality with the most striking clearness and to remain distinct, but they spread out

branching limbs toward one another, "dendrites" as they were called, which, however, could not be seen to touch each other. It was accordingly assumed that, when the visual cells are stimulated, their dendrites are able, by "intermittent contact," to convey the stimulus to the apposed dendrites of the "bipolar cells" and these, through their proximal dendrites, to pass it on to the dendrites of the "multipolar cells." A bewildering number of differently shaped dendrites were found and attempts were made to classify the cells accordingly. It was claimed that there must be regular chains of cells carrying dendrites, no two of which are alike, and that these link the rods with the nerves. The absence of any single link would, it was thought, cause a blind spot.

This application of the neurone theory is the most recent development of the "cell" doctrine as regards the retina. It is of special interest, because it seems to explain this standing riddle of the retina, and because it appears to solve in a plausible manner the problem of nerve connections in the retina. It strongly supports the cell-doctrine, for the individuality of the cells as distinct living organisms, even though united into tissues, is emphasised by it probably more clearly than ever before. It need surprise no one, therefore, that the neurone doctrine was almost universally received with acclamation.

If it can be shown that the solution of the retina afforded by the neurone theory is erroneous, we shall have done much to justify the criticisms of that theory which have already been advanced by other writers on this subject.

Let me now describe the retina according to the protomitomic theory, which not only explains the

appearances but enables us to answer questions as to the finer structure and physiology of the retina which the cell doctrine, even supported by the neurone theory, completely fails to do.

One of the first results of a comparative study of retinas is to show that what are called "cells" in the vertebrate retina do not fulfil the essential requirements of cells.¹ They are not masses of cytoplasm

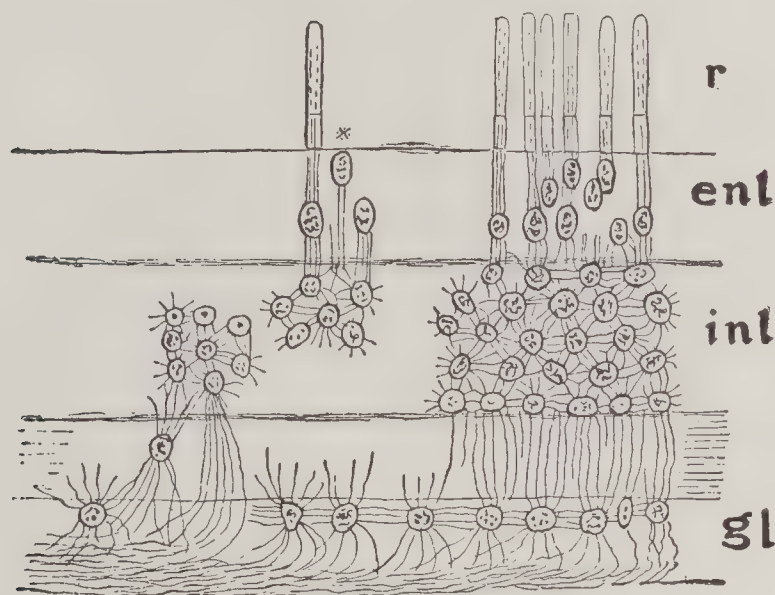


FIG. 34

Diagram showing how the primitive nerve fibrillæ reach the rods through the intermediary of the retinal protomitotic system. r, rods; enl, external nuclear layer; inl, inner nuclear layer; gl, ganglionic layer.

containing nuclei, but are primarily nuclei, suspended in some way among the meshes of a cytoplasmic syncytial framework (Fig. 34). The nucleus, according to the universally accepted cell doctrine, is an organ

¹ For the detailed description of these researches, see "Studies in the Retina," pts. i-vi, in the *Quart. Journ. Micros. Sci.*, vols. 43-47. And here I may add that many of the more important conclusions on which I specially rely for my theory have been recently confirmed by Dr. John Cameron; see *Journ., Ant. and Phys.*, 1905, pp. 144-146.

of the cell, and to have nuclei without cells is like finding live hearts, or livers or stomachs without any bodies to which they belong. Nevertheless, it is

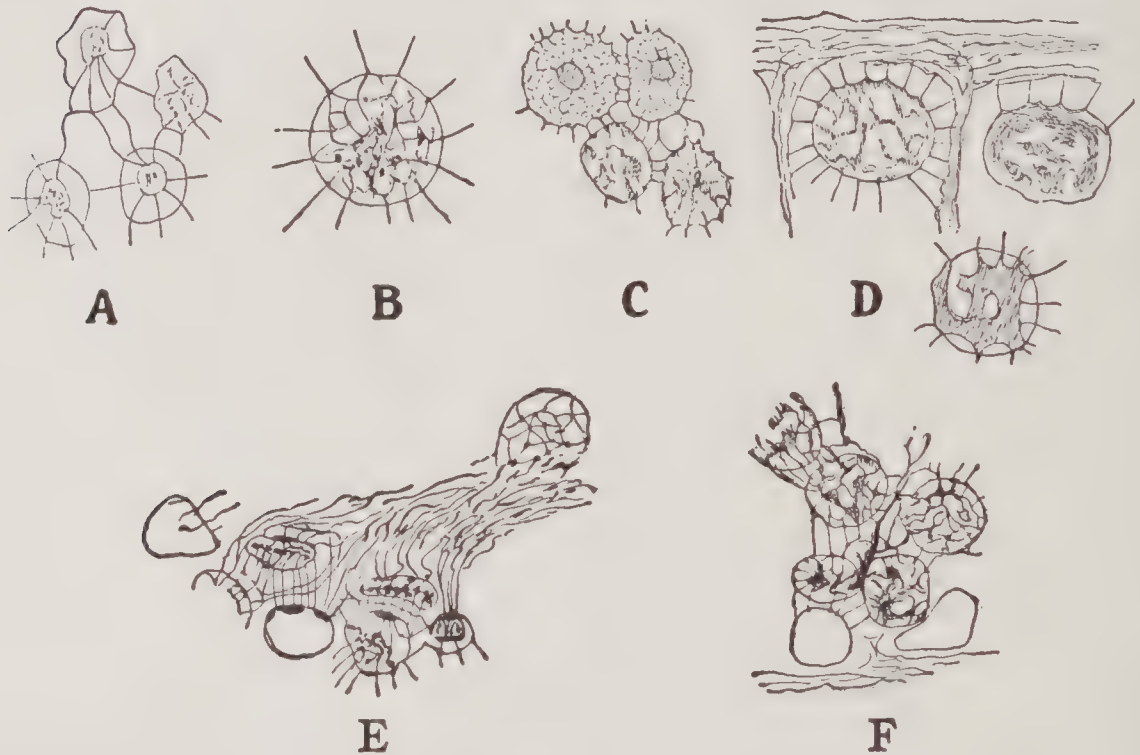


FIG. 35

- A.-D. Visible elements (nuclei) of the middle layer of the retina. These are all seen united by filaments which run into the nuclei and in each case, the chromatin is differently distributed; in A, it is balled together in the centre; in D, several stages of this balling seem to be represented. The points round the periphery from which the connecting filaments depart are shown in C and D.
- E. Retinal nuclei devoid of cytoplasm connected together by the filaments. The deeply staining nerve fibrils become faint before reaching the nuclei, but the connection can be made out.
- F. (From the Amphibian retina.) Nuclei joined together by the filaments, which are made visible by clumps and coatings of staining matter. Irregular clumps of extra-nuclear chromatin are massed on some of the filaments in this preparation.

apparently matter of accident whether the nuclei of the retina have or have not granular cytoplasm massed round them; the vast majority have none and are simple nuclei. Where present, the cytoplasm is found in very varying quantities and shapes. It is most

often associated with nuclei of the innermost layer and is abundant only in the retinas of the higher Vertebrates, where it occurs in sufficient quantity to give rise to the familiar diagram of the "multipolar ganglionic cell." This diagram, founded solely upon special cases has been accepted and these cells regarded as essential factors of retinal structure, whereas a more extended comparison would have shown that the only essential part is the nucleus.

With regard to those cases in which the granular cytoplasm is associated with the nuclei in lesser quantities, an arrangement in any way suggesting a "cell-body" *containing* a nucleus is rarely seen. The essential structural element is obviously the nucleus with what appears to be a larger or smaller wisp of cytoplasm clinging to it, and not seldom of a shape suggestive of its streaming away distally, *i.e.*, toward the rods.

The same is the case with the nuclei of the middle layer. Here the uneasiness of the earlier describers is evidenced by the name "granules." These granules being, however, regarded as cells, are, as above described, diagrammatically represented as suspended on spindle-shaped threads of cytoplasm radially arranged. This again is not supported by renewed research. A few such appearances may be found, but very few. An extended comparison shows that the middle layer consists of nuclei often closely packed together, with no other trace of cytoplasm near them than the thin strands and membranes which belong to the general syncytial framework just mentioned. (Fig. 35 A-F.)

The elements of the outermost layer, in the lower Vertebrates at least (frogs, salamanders, etc.) in which the rod-nuclei are in single rows, better fulfil the conditions of "cells," inasmuch as it is possible to regard

the whole rod as the "cell body" with a nucleus at its base. But, as we shall see later on, the development of the rods shows them to be no more true cells than are the elements of either the middle or the innermost layers. *There are, in fact, no "cells" in the retina, but only nuclei; we obtain the appearance of cells as it were merely by accident, i.e.,* when a sufficient quantity of cytoplasm happens to surround one of the nuclei. For the phenomenon that has been called a "cell" is merely a nuclear node of a network round which nutritive and other matters have congregated.

We have hitherto, in this work, been dealing with tissues in which the reticulum is obscured, only traces of it being seen—mere hints being given, in this fact or in that, but so persistently and in such varying ways that no impartial person can doubt its existence. Here, in the retina, we have the nuclear network largely free from all obscuring cytoplasmic matters and the question is, can it be seen?

It was, as a matter of fact, in the retina that I first saw it, and only afterwards were the traces of it sought for in other tissues and found in abundance.

On discovering the nuclei not embedded in cytoplasm, the question naturally arose, If not embedded in cell bodies, as the organs of cells, how are the nuclei suspended? and what are the mutual relations of the nuclei and the cytoplasm? Only slowly did I arrive at the answers to these questions. At first I fell back upon the retinal framework; was it possible to regard its strands as representing the cytoplasm belonging to the nuclei and holding them in place? Closer study showed me that these strands are too variable, sometimes present in considerable quantities, at others hardly demonstrable. Further, when present, they

very rarely touch the nuclei, but always pass between them. When however they do touch, the effect on the nucleus is somewhat startling, as will be described below. Groups of nuclei may also be seen without any of the cytoplasmic strands running in between them. The strands seem to appear when the nuclei are scanty and far apart; when the latter are crowded together, as in embryonic eyes, none are, as a rule, to be seen.

These facts, that the nuclei, as a rule, have no masses of cytoplasm in which they are embedded and are, further, not in contact with any part of the retinal framework, made the puzzle of their suspension still greater, for it was obvious that they must be supported in some way. The solution of this difficulty is supplied by the protomitomic network which came to light in this way.

Following up a very early observation, I looked systematically for very fine fibrils which I had occasionally seen running from nucleus to nucleus, but not often enough to lead me to regard them as of great biological importance. Many preparations showed no trace of them whatever. But the gleanings of several years convinced me that the occasional appearance of these fibrils was to be explained on the assumption that a regular system of such internuclear connecting filaments exists in life, but is destroyed during the preparation of the tissues, the filaments being perhaps ruptured by the suddenness of the reactions of the living substances to the fixatives. Further, it was obvious that, even if the filaments are preserved, their invisibility could be accounted for by their extreme delicacy, which renders them at all times liable to be obscured by the denser surrounding substances. Even when they are not thus obscured, they are only visible in their simple

hyaline condition under the very highest powers of the microscope and the most favourable conditions of lighting.

Time confirmed this conviction, for, though the majority of preparations only showed the connections between scattered nuclei, I was fortunate enough, from time to time, to find one which showed considerable tracts with the network preserved. In such a case, it was evident that the network owed its visibility to the fact of the filaments being coated, sometimes even thickly clotted, with staining matter, presumably chromatin, spreading from the nuclei beyond the nuclear membrane on to the filaments. In the retina, this matter was evidently travelling outward toward the rods. On this streaming of the chromatin along the protomitotic network to the centres of the greatest physiological activity much has already been said. For the present, we are chiefly concerned with the fact that this process may at any time show us the protomitotic network very clearly. Even when the filaments themselves are quite obscured by cytoplasmic matter, their courses through the cytoplasm can at times be traced with ease by the rows of beads or continuous streams of chromatin threaded upon them. (See Fig. 31, C.)

Now, while these internuclear filaments solved the problem of nuclear suspension, the interest they aroused on their own account put that problem quite into the shade. Mere suspensory filaments they certainly were not; this was obvious from the following facts: the chromatin leaves the nuclei and wanders away along them; they can easily be seen to be continuations beyond the nuclear surface of filaments of the intranuclear reticulum; and, most conclusive of all, they can be

seen to run through the reticular layers and to join all the nuclei of the retina together into a continuous *nuclear system*. There was thus revealed a *delicate linin network underlying the whole of the visible cytoplasmic mass of the retina*. This is gathered at intervals into more condensed networks—the nuclei, within which the chromatin is usually collected and from which it can travel down the filaments.

This is how I first discovered the protomitomic network. It was seen at once to be a possible clue to many unsolved biological problems, if only its universality could be established. It seemed just possible that it might be a structural feature in the retina alone, but this was highly improbable. The nuclei of the retina were ordinary nuclei and, except in its production of rods, there was no striking difference between the retinal epithelium and other many-layered epithelia.

It was, however, clearly a first duty to see whether its universality could be placed beyond the merely probable, and this work is the result of my efforts in this direction, and now, to the evidence, direct and indirect, already given in earlier chapters, we add this evidence that the network can actually be seen in a tissue in which the nuclei happen to be, as a rule, quite free from cytoplasm.

The retina not only reveals the existence of the network but permits us to gather many interesting facts about it, and these, it is important to note, fall into their places in the scheme which we have been able to build up in earlier chapters. A few of the more important of these points of agreement may be given here.

In earlier chapters, we have noted the movement of the chromidia along the filaments so as to collect into

groups, a process which resulted in the formation of the central nucleus. From these central nuclei, the chromatin masses which, there is reason to believe, are aggregations of chromidia, travel outward for the formation of yolk and other excretions, and all the evidence seems to point to this matter travelling *along the filaments*. In the retina, the chromatin can actually be seen on the filaments, making them visible. It is here required for the functioning of the rods, although in what capacity we do not know. All we actually know is that it passes into them along the filaments in constant streams and must be used up in them.

But this is not the only instance of matter travelling along the filaments in the retina. The rods absorb matter consisting, in part at least, of the pigmented granules of the choroid epithelium into which their tips are plunged. Now, this matter has to escape outward, *i.e.* through the retina. It is interesting to note that it travels along the cytoplasmic strands, gradually establishing for itself paths, which become more and more pronounced with advancing age and give rise to what are known as Müller's fibres. Now, if we take this fact in conjunction with the observation, previously noted, that these cytoplasmic strands seldom come into contact with the nuclei, and then not without seriously affecting them, we obtain a possible answer to an important question which was left unanswered in the chapter on the epidermis.

It was there stated that streams of waste matter, with occasional pigment granules, pass outward so as to supply matter for the horny surface, and that the chromatin out of the epidermal nuclei seems to be carried along with this waste matter, being probably needed

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as an active element in the formation of horn. The parallel between this and the process just described for the retina is obvious. We have the waste matter with pigmented granules passing outward in both; in the retina, the granules pass into the rods, where they can mingle with the chromatin which has, as it were, come down in quantities to meet them. The matter is clarified in the rods as it is in the epidermis in the *stratum lucidum*. In the retina, however, it does not dry into horn as it does in the epidermis, but streams further outward and into the vitreous humor, to whose substance it clearly contributes.

But the question of greatest interest with regard to the epidermis left unsettled was whether the streams of matter passing along the filaments inhibited their elementary nervous functions. We saw some reason to believe that a partial inhibition was at least very probable, inasmuch as the streams seemed to undergo considerable modification in primitive sensory organs, which are, as a rule, associated with secretions. The retina supplies us, I believe, with further evidence. If it is possible to regard the cytoplasmic strands as also composed of fundamental filaments early specialised out of the network, we should then have two systems of filaments in the retina: one set passing through the nuclei and carrying chromatin into the rods, and another set carrying streams of waste matter outward, carefully avoiding the nuclei and, apparently, also even any large masses of chromatin which they meet. Indeed this interlocking of the two streams, which yet have to avoid one another, will explain a retinal phenomenon which I found very puzzling (see the diagram, Fig. 34). And I may here mention that, when a nucleus comes into contact with one of the Müller's fibres, as these

streams of waste may be called, it is sometimes very obvious that its chromatin is passing out of it and mingling with the stream. In some places, the nucleus is itself drawn out into a long point into the stream, at others, the chromatin granules in the nucleus are individually stretched outward and laterally toward a stream which has touched its side. These are rather common phenomena in the retina of the Frog, as the Müller's fibres become pronounced.

We have here, then, not only the fact that the streams absorb chromatin, but the more important point that they travel along special systems of filaments, avoiding those which may be regarded as having their nervous functions specialised, and we may infer therefrom that such streams would tend to inhibit such functions. On the other hand, we gather that the streaming of chromatin outward along these nervous filaments evidently does not inhibit their functions. But this is not all. We began with an "if"—if we could show that the cytoplasmic strands were a specialised part of the reticulum, we should certainly have some evidence for this interpretation. We should, in the first place, have the synthetic activities of the filaments as the cause of the streaming and, in the second place, they would be homologous with the filaments along which the streams of waste matter travel outward through the epidermis.

In my work on the development of the retina, I traced these cytoplasmic strands, both those stretched between the nuclei and those forming the matted reticular layers, from the cytoplasmic matter which once surrounded the nuclei where they were arranged in a single layer as they are round the rim of the retinal cup. This is what the appearances point to, but, un-

derlying this cytoplasmic matter, there must surely, in the nature of the case, have been filaments of the network (see Fig. 34). Although I did not see it at the time, such filaments seem to be required in order to account for the fact that they can be drawn out and stretched and re-arranged in the manner I have described. And now, indeed, the matter has been set at rest quite independently by Dr Cameron,¹ who has pointed out that the developmental strands which are thus re-arranged into the so-called cytoplasmic framework of the retina come directly from the nuclei. I had myself neither noticed this fact under the microscope nor perceived it theoretically.

These arguments are, I admit, highly technical, but that cannot, I fear, be avoided. The points are of great importance, for they yield us further insight into the forms and functions of the protomitomic network. I may here briefly sum them up by saying that the vertebrate retina shows us in detail an arrangement of the filaments of the network so as to form two systems, one specialised for carrying away streams of waste matter, and the other freed from such streams and therefore capable of specialisation for nervous functions. These were both points that came up for discussion in the chapter on the condition and functions of the network in the epidermis.

We can now take up another point on which the retina has thrown further light. In Chapter XI, a scheme was developed for the explanation of the morphology of the nervous system in which that system figured as the residuum of the network after all the rest had been separated off into organs and tissues specialised

¹ *Journ. Anat. and Physiology*, 1905, pp. 144-146.

for other functions, and thus having the nervous functions of their filaments partially or completely inhibited. We may doubtless assume that as, in the course of this process, the nervous functions were more and more confined to this residuum, its texture gradually underwent progressive specialisation for increasing efficiency. This account of the origin of the central nervous system explained the fact that it united all the organs together into a complex. The strands of connection are strands of the network, the chief constituents of which are the elementary filaments conveying the stimuli. I return to this subject here because the retina supplies us with a perfect confirmation of our scheme. In it, the network can be seen gathered into nodes and, from the innermost layer of nodes, the filaments are visible streaming away to form the retinal nerve which connects the retina with the central system. Distally, the filaments stream down the rods, where they are stimulated, as I believe mechanically, by the waste matter which forces its way between them along processes of the choroidal energids.

Not only does the nervous system of the retina fall thus simply into its place in our general scheme, but we may learn something from it as to the texture of the central system. We have seen that, in the retina, the filaments along which the nerve currents have to pass are kept free from the streams of waste matter travelling along an entirely different set of filaments. Now, if this is a necessity in the retina, it is also a necessity in other parts where the nerve functions are required at their best. There is no danger in the central system of such tremendous streams of waste matter as come pouring through the epidermis and

retina, situated as they are near the surface, but some waste there must always be, as the result of any and all functional activity, and I would suggest that, in the central nervous system, we have to differentiate between the filaments carrying stimuli and those along which the streams of waste are being carried away. I suggest therefore that we must regard the "Punktsubstanz" of the central nervous system in the brain and spinal chord, as in the retina, as a fine interlacing and entanglement of the two systems of filaments, but arranged so as to flow past one another with the least possible contact.

And here let me say my last word on the neurone theory and its methods of differentiating the tissues. The figures of the retina, published in support of that theory, do not differentiate between the two systems we have described. The Müller's fibres, the specialised streams of waste, are stained and the cytoplasmic strands, especially those running to or from the cytoplasmic masses round the nuclei, are also stained, but these are not nervous; on the other hand, the exquisite filaments coming from the nuclei and running from nucleus to nucleus and down rods are not stained; these are the nerves. The contest between us thus rests upon this one point: are there such nuclear linin filaments as fundamental elements in protoplasmic structure or are there not? I have endeavored throughout this work to show that there are, and that they give us a more intelligible account of the phenomena of life and of organic structure than the cell doctrine ever can give. If this is correct, the phenomena of the neuronists require re-interpreting, for what they are calling nerves are not nerves but, in some cases at least and perhaps in all, streams of waste or other

cytoplasmic matter. And I will here add that the case against the neurone theory will be found equally strong if the reader will compare the details of other sense organs now to be described according to the protomitomic theory with the account of the nerve supply of those organs according to the neurone theory. This comparison I leave the reader to make for himself.

From this account of the retina and the confirmation it has afforded of my suggestion that the peripheral filaments of the network are all essentially nervous, let us pass on to consider sensory organs that are more obviously modifications of the epidermis than the retina. My suggestion, it will be remembered, was that the primitive nerve functions of the filaments that run through the epidermis are inhibited by the streams of matter which travel along them as material for the cornification of the outermost layers of energids. There are certain indications of arrangement in the retina for the supply of definite paths for the waste matters, so that these shall not interfere with the elementary nervous functions of the filaments coming from the optic nerve and running down the rods. We shall now take two portions of the epidermis undoubtedly specialised into sense organs, the olfactory epithelium and the gustatory buds, and examine them from the new points of view.

According to the protomitomic theory, the network of filaments underlying the epithelium and appearing at the surface in some cases at least, as fine cilia-like processes, is sensory, *i.e.*, the whole network is sensory. If so, it is obvious that the filaments are no longer available for the passage of the waste matters

which try to escape outward through all the surfaces of the body. Having to find another way, they have collected in spaces of the network underneath the epidermis, there giving rise to glands which open through special ducts without disturbing the sensory functions of the filaments. But is there any evidence that the filaments running through the epidermis form, in the case of the olfactory organs, a network such as we have described for the rest of the epidermis and for the retina? The usual description certainly admits of this supposition. In Fig. 36, of the nasal olfactory epithelium, the thicker epithelia "cells" represent nothing more than the thicker bundles of filaments coming through the outermost layer of nuclei, the thinner "cells," the thinner bundles coming up between the outermost nuclei. This is certainly a simpler supposition than that these are "cells," each playing some different part.

The difference between earlier descriptions of the retina and facts as I found them leads me once more to doubt the existence of so many clearly defined individual elements as are represented by Max Schultze's beautiful figures.¹ But, at the same time, while maintaining that the whole of the olfactory epithelium is in reality a network, I would not deny that there may



FIG. 36

Diagram of the arrangement of the sensory nerve fibres in the olfactory organ and bulb (after Retzius)

¹ "Bau der Nasenschleimhaut." *Abh. d. Nat. Ges. zu Halle.* Band 7, 1863.

be streams of albuminous matter coating the filaments and massed around the nuclei and giving the appearances of the long "cells" described by Max Schultze, or, again, that in the fixing of the material, the albuminous matter coagulated in this manner round the nuclei and upon the filaments of the network.

In order to satisfy myself that this continuous network underlay all the appearances of cells here, as in

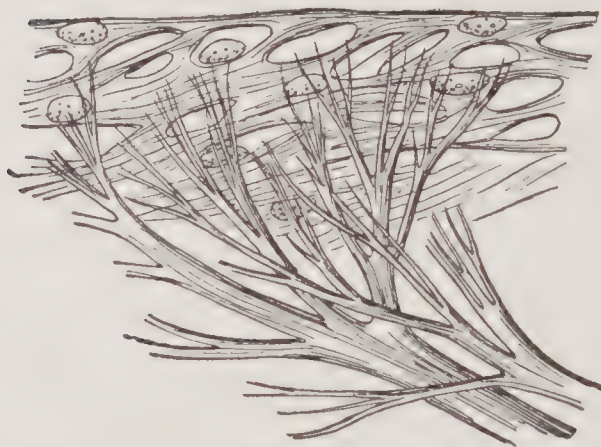


FIG. 37

The opening out of a bundle of nerve fibrillæ into the nasal olfactory epithelium. (after Max Schultze *Bau der Nasenschleimhaut; Abh. d. Nat. Ges. zu Halle.* Bd. 7, 1863.)

the retina, I made a careful microscopic study of this epithelium in a young tadpole, and found the network quite easy to trace, owing to the fact that the filaments connecting the nuclei were beaded with minute round granules of yellowish pigment. These rows of pigment granules were the

homologues of the prickles of the ordinary epidermis, only, instead of the waste matter passing in continuous streams, it passes as beads.

Lastly, we have one more direct argument, founded on Max Schultze's illustration of the opening out of the bundle of nerve fibrillæ into this epithelium (Fig. 37). Can there be any doubt that these fibrils of the nerve run on continuously into the filaments of the sensory network, or that we here have the same phenomenon as that described for the retina, except that, in this case, the nerve runs directly into the sensory layer before it opens out and then bends back for its ulti-

mate fibrils to join with the filaments of the retinal network?

Still simpler is the explanation our theory gives us of the specialisation of the external layer of the surface for the formation of organs of taste; the gustatory buds, as they are called. Fig. 38 shows such a bud, which I interpret as a small portion of the network that has retained its primitive nerve functions by becoming isolated from the rest of the network of the epidermis, the latter having become specialised for the conveyance outward and the utilisation of waste matter. The filaments of each sensory portion of the epidermis gather together proximally and pass, still more or less isolated, through the corium as a nerve strand with its bundle of primitive fibrillæ and, uniting with other strands, run as such to the central nerve mass. Distally, they are gathered together into a bundle of small processes which project slightly above the surface, so as to come into contact with the surrounding medium. The nervous functions of the filaments of the gustatory buds are thus protected from the inhibiting effect of streams of waste matter by being isolated all the way from the surface to the central nervous system. At the very surface, they open out into a bud-like body, with a certain number of nuclear nodes, just before they project beyond the morphological surface.

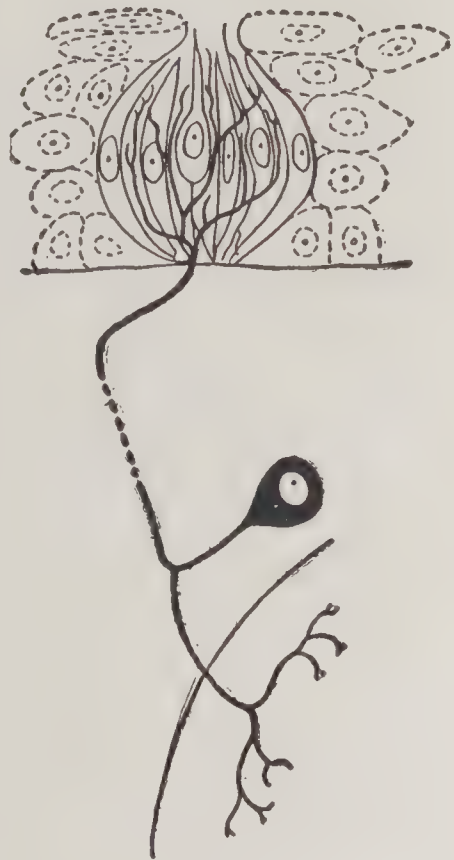


FIG. 38

Gustatory bud of a Vertebrate (after Retzius.)

CHAPTER XIII

THE PHENOMENA OF GROWTH

IN the earlier chapters of this work we have analysed many of the principal forms of life and the fine textures of their component tissues, and I claim that the theory of an underlying linin-chromatin network has explained the ascertained facts better than the cell-colony theory has ever done. In turning to one of the vital processes exhibited by these organisms, that of growth, we shall again find that the ordinary cell-colony theory, with its union of so many separate units, is too rigid a medium for our imaginations to work in, whereas our network of linin threads enables us to give a fairly intelligent account of what takes place.

Growth, biologically, embraces not only the increase in size of the individual with all its complications, but the multiplication of those individuals, each in the likeness of its kind.

This subject has already been touched upon in Chapters II–IV when tracing the gradual evolution of a metaplast upward from our hypothetical unit; growth is but the evolutionary process shortened and condensed.

According to the cell-colony theory, growth starts with the cell as the unit, and this, in a way, places the cell itself outside the range of the analysis of growth processes. This is unfortunate, for it is clear that, in any growing metaplast, the growth of the individual

cells from which it is supposed to start precedes the division and multiplication of the whole organism. The general assumption seems to be that the growth of the individual cell is a process *sui generis*, while that of the metaplast is a colony formation. This means not one phenomenon but two phenomena, neither of them understood. For the vital process of growth within the cell is totally unknown, and the other, colony formation, presents us with the insuperable difficulty of secondary co-ordination of an aggregate of separate individuals into an organic whole (see p. 82).

This interruption in growth, this sudden change of principle is not needed if we start from a simpler unit. An element that admits of analysis, the chromidial unit, yields us the central chromidium, its radiating filaments and the fluid matter. The growth of the latter need not trouble us, since it has no organic structure; we have only to follow that of the chromatin and the filaments. The whole of growth, from first to last, indeed, can be shown to be essentially the growth of these two substances, with certain variations only in the resulting appearances. The interpretation and change of principle required by the cell-colony theory to account for the sudden appearance of nuclear division in the growth of organisms with developed nuclei is not needed, for this appearance in no way affects the essential principle.¹

According to the protomitomic theory, the structural factors are the chromatin and the linin threads. That the larger masses of chromatin consist of chromidia is now and then made evident by the breaking up of

¹ The biophor theory, which relies upon colony formation as the sole principle of growth both in the cell and metaplast, runs against the difficulty of co-ordination twice instead of once.

such masses into multitudes of small bodies not visibly differing from the hypothetical chromidium of our theory.¹ The chromidium grows, as we have seen, by the assimilation of material from its medium; when it has attained a certain size, it divides into two. This early division of the chromidium seems to be constant enough to justify us in provisionally regarding it as in some way inherent in its constitution, *i.e.*, physically necessitated.

The original chromidium of the unit, before it divided in this way had, we saw, a certain number of filaments radiating from it. The question is, what was the fate of these? We can of course understand their growth in length, and can well imagine that this growth was limited, the filament not stretching, as a free, naked filament, beyond a certain length from its chromidial centre. But when the chromidium divided, how would the filaments be rearranged? The result of growth, *i.e.*, of repeated division of the chromidia with division and re-arrangement of the filaments, appears to be a filamentous network with chromidia at the nodes, but how this arrangement could come about has been a matter of conjecture. The method suggested in the sketch given on p. 17 is that, as the chromidia move apart, new filaments grow out between them and near the line joining their centres, while all the rays which stand out at (or nearly at) right angles to this line split

¹ This has been discovered microscopically with reference to some of the large chromosomes seen in dividing nuclei. It may also be inferred from the fact that, when chromatin escapes from the nuclei, in order to disperse along the network, either for the formation of yolk or as in the "Nissl's Schollen," it always breaks up into clouds of these small bodies. Their appearance in dense masses may, on our theory, be taken as an indication of the closeness and density of the network that unites them.

longitudinally. The repetition of this process would obviously result in a network such as is postulated by the theory.

In Fig. 39, E, p. 256, this network is shown as symmetrically rectangular, but this could hardly ever be the case in nature, since different amounts and rules of growth of different parts and the varying strains put upon the filaments would be felt from the first.

The earliest and most undifferentiated masses of protoplasm thus grew, I believe, by the growth and regular division of the masses of chromatin accompanied by growth in length, and by the longitudinal splitting of the filaments radiating from these.

The primitive network described in Chapter I might, apparently, grow in this way to a great size, but its inherent responsiveness to the environment would not allow it to remain undifferentiated. Its very existence would depend upon the efficiency of its responses to attractive or repulsive stimuli, and these would necessarily lead to a concentration of its contractile and nervous energies. Working along these lines, we gradually arrived, in our sketch, at the typical cell, in which the chromidia are, to a great extent, concentrated and stored in a central nucleus and, from this central organ, the filaments of the network radiate to the periphery. I need not here go over the steps again, because all the larger organisms whose growth most interests us begin at this high level of organisation called the cell.

Arrived at the cell, our theory requires no such change of principle as is implied in the colony formation of the cell doctrine. We have, instead, a continuous process. Any change such as the appearance of nuclear division is due solely to the fact that the materials

with which growth has to deal are now more complicated. Instead of the single chromidium, we now have the vesicular nucleus with its store of chromidia co-ordinated on some definite plan upon a close network of filaments, and instead of the simple stellate arrangement of filaments, we have a complicated network with the bulk of its strands arranged radially round and in definite association with the nucleus. This far greater structural complication of the cell necessarily entails profound changes in the details of the growth processes, but the principle is essentially the same. *The chromatin centres increase in number by division and the filaments lengthen and split.*

But before going into these new and altered details in the growth processes, it is necessary for their comprehension to realise the meaning of some of the changes in the organism itself which were accomplished when it became a cell. Instead of the simple uniform network with distributed chromatin, we have, in the protoplast, a highly organised network, arranged for the highest possible functional activity that can be called forth in so minute an organism by the environment. The rearranged network, as a network, has now become the prime morphological factor, while the chromidia are massed together on a central condensed tangle, which functions not only as a storehouse for the chromatin required by the network for its activities, but also as a co-ordinating centre for its nerve stimuli. We have then, I repeat, primarily a network with a central organ; we again have a unit recalling, but on a much higher scale, our hypothetical unit with its central chromidium and radiating filaments.

In dealing with the growth of the individual organ-

ism, we have two cases to consider; (1) that of a uninucleate organism which has merely to grow in size without any change in its organisation, and (2) that of such a uninucleate organism as an egg which, in growing, has to develop into some complicated multinucleate organism.

1. The mere growth in size of a uninucleate organism may be referred to a slight lengthening of the filaments of the network, either throughout the whole of its extranuclear portion, or simply round the periphery. In the former case, we should have to postulate an increase in the amount of matter deposited on the tips of the peripheral filaments so as to keep the ectoplasm compact, perhaps also an actual increase in the number of filaments. Where growth is confined to the periphery, we should have to postulate a continual onward shifting of the materials in order to keep them always at the tips. This principle of the shifting of skeletal matter along the filaments has already been illustrated under even more complicated circumstances and need not therefore be further discussed here. All that is required in the kind of growth under consideration is increase in size without further complexity of organisation. So far as I can see, there need be no great difficulty in understanding this process.

2. It is otherwise when an egg has to grow into a highly complicated metaplast. Life is hardly long enough to read all that has been written on the problems involved. I do not claim that the new theory solves any one of them, only that, as it supplies us with certain fairly well defined factors, such as the fundamental filaments and the chromidia, we have material with which the mind in its speculative processes can

deal. So as to avoid being too discursive and being drawn into discussions of some of the minor and yet in all cases fascinating problems which arise at every turn, we must here confine ourselves rigidly to the chief points: the growth of the filaments and the division of the nuclei.

Little need be said as to the division of the filaments, which has already been mentioned many times. The growth of the rods in the retina may be given as an instance. These rods begin as minute vesicular protruberances from the proximal end of nuclei and grow out to as much as 50μ in length with filaments accompanying them right to their tips, a phenomenon that can only be accounted for by the growth in length of the filaments. Such growth in length may, indeed, be considered as one of the inherent properties of the filaments. The question above raised as to whether they can grow indefinitely, free and naked as in the hypothetical unit, does not here concern us for, in these larger organisms, chromidia may follow the growing filaments down along their length, so that the tip need never be far from a chromidium. This is quite in keeping with observation, for the filaments running down in the wall of a growing rod are often only discoverable from the fact that they are beaded with minute staining points. The fact that the filaments grow in length can thus, I think, be accepted without any further demonstration, and we turn to the more difficult subject of the divisions of the nuclei, in the course of which we shall not only find further evidence for the growth of the filaments in length but also for their longitudinal splitting.

The apparently universal method for the increase in number of nuclei is for the existing nuclei to divide,

the result being that two nuclei appear where there was formerly one. In the absence of any clear idea of what is involved in the process of nuclear division, it has naturally been considered as the most startling and inexplicable phenomenon in the growth of living matter, indeed, it has been regarded with awe, as if we were peering at something the explanation of which is lost in the ultimate mystery of life. It is, therefore, to my mind, one of the strongest evidences in favour of the protomitotic theory that it indicates a way of explaining this process, causing the phenomena to stand out as a perfectly intelligible mechanical device, as clear of the ultimate mystery of life as any of the other more familiar physiological processes. Indeed, I have reason to hope that, with the clue yielded by the protomitotic theory, the phenomena may, in the near future, be still further elucidated.¹

It is impossible, within the limits of a short chapter in this sketch to deal with one-fiftieth part of the views and observations expressed and described since the phenomena of what is called "mitotic"² division first began to be properly investigated in the seventies. I must confine myself to just so much as seems to me necessary to our immediate argument.

We have, first, the fact of the appearance and subsequent disappearance of the filaments, and, secondly, the form they assume. Let us see what light our theory can throw upon these two points.

The fact of the appearance and disappearance of the

¹ See Cameron, *Journ. Anat. and Phys.*, 1905, pp. 144-146.

² The name mitotic refers to the fact that, at the time of division, a vast number of filaments not previously visible appear, assume a certain typical and very striking arrangement and then on the streaming of the chromatin, usually again disappear.

protomitomic filaments must by this time be familiar to all readers of this book. So mysterious did these apparitions seem to upholders of the cell doctrine that the desperate hypothesis was resorted to that the fibrils are specially developed for the purpose of dividing the cell and that they dissolve again as soon as their work is done! Those, however, who believed in the fibrillar structure of protoplasm rightly saw, in their sudden apparition, corroborations of their doctrine but hardly, one would think, of the doctrine that the cytoplasmic fibrils are distinct from and unconnected with those of the nucleus.

The true causes of the apparition of filaments which are ordinarily invisible have already been explained. Some substance which takes stain, streaming along them, renders them visible. In many of the cases described, streams or small beads or shapeless clots of chromatin brought the position of the threads into view; in *Volvox*, it is some cytoplasmic matter; in what are called the "prickle cells" of the human epidermis, it is material for the production of horn; in the brains of very young tadpoles, short nuclear connections seem to be thickened by the yellow matter that forms the pigment granules. What that matter is which coats the threads in the division figure and makes them visible has still to be discovered, but that what we see is not the fundamental filaments themselves we gather from the facts that the threads are too thick and irregular, and that some cases are known in which, after the division and consequent rearrangement of the filaments, a cast of part of the division figure, viz., of the "spindle" may be found lying rejected in the cytoplasm. The most probable view is that, during division, the chromatin bodies get rid

of all accidental products that have been taken in during their activities and that these spread out along the filaments.

It is clear that, for any right understanding of the process under consideration, it is necessary to discriminate between the non-essential matters that take stain and the fundamental filaments. The former have often been called linin, whereas it is clear that they are accidental and only for a time seem to indicate the courses of the true linin or protomitomic filaments. How valuable the distinction is we gather from the fact that it enables us to understand such a difficult phenomenon as the rejected spindle.

But it is when we turn to the second point, to the forms and patterns assumed by the threads during the process of division that we have the most startling confirmation of the protomitomic theory. It is true that there may be variations in these forms not yet easy to account for. But if we can show that the most common type of the division figure, the familiar spindle, the ends of which coincide with the centres of two asters is, at least in many of its more important details, exactly what the protomitomic theory demands, we shall have, it seems to me, an absolute demonstration that we are at least on the right track towards the ultimate elucidation of the whole phenomenon.

We seem to obtain light upon the figure the moment we realise that the two essential structural factors of the protoplast or energid are a network and so many chromidia distributed upon the filaments. The latter are no longer found only singly at the nodes but are also stored in vast quantities in a central tangle of the network, the nucleus. Now, of these two factors, the network is clearly the chief morphological factor; on

its form and arrangement depend all the possibilities of contraction and sensation, conveyance of material, skeletal formation and, in fact, the special character of all the vital processes exhibited by the organism. It is obvious, therefore, that, if any protoplast has to divide into two exactly similar halves, this network must divide into two exactly similarly arranged networks or, if an energid, or, let us say rather, a nucleus has to divide, which already has a definite place in the network of an organism, the division must result in an increase in the amount of the network, but in no way disturb the fundamental arrangement of the established lines for the contractile and nervous energies of the part of the organism in which it is situated; the single nucleus must therefore divide accurately into two nuclei, and the problem is how to divide a complicated network into two exactly similar networks?

This is a difficult problem because, even if we could imagine every thread composing the network split longitudinally in such a way as to yield two exactly similar networks, we should still have no means of disentangling the two; by no conceivable process could we get one outside the other without the rupture of almost every filament.

Light on this subject first came to me before I had discovered the fundamental network. I noticed that, in the retina, the nuclei that divided were always, morphologically, peripheral nuclei and that their division must mean a multiplication of nerve fibrils running distally outward, in order some day to run down the rod which such a nucleus would certainly produce. But the nucleus was a network; hence the process of nuclear division must be some device for dividing a three-dimensional network into two separate halves

without rupturing the organic continuity of the filaments of which it was composed. Reasoning upon these lines, the following diagrammatic explanation of the process came into my mind.

Let $a b c$ in Fig. 39, A, represent three filaments running outward to a surface and supplying the part x, y , as potential nerve fibrils to supply a rod which will some day project through x, y . Each, as part of a network, is organically connected through the nucleus N from which they proceed, by a certain number (say three) of lateral filaments running tangentially into the adjoining nuclei n', n'' , and also by three filaments with the central system C ; so that any stimulus applied at either of the points of the

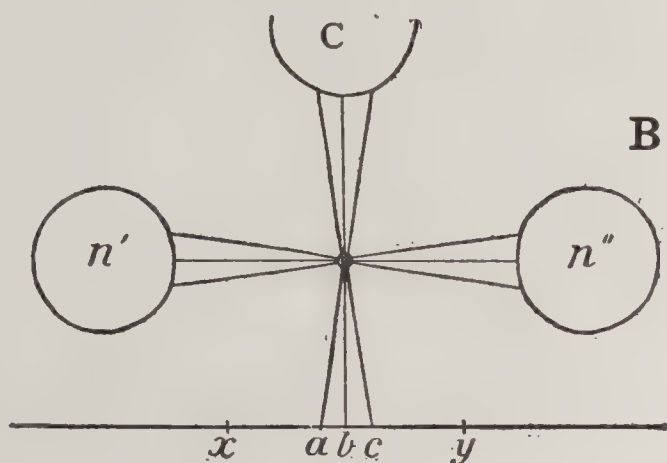
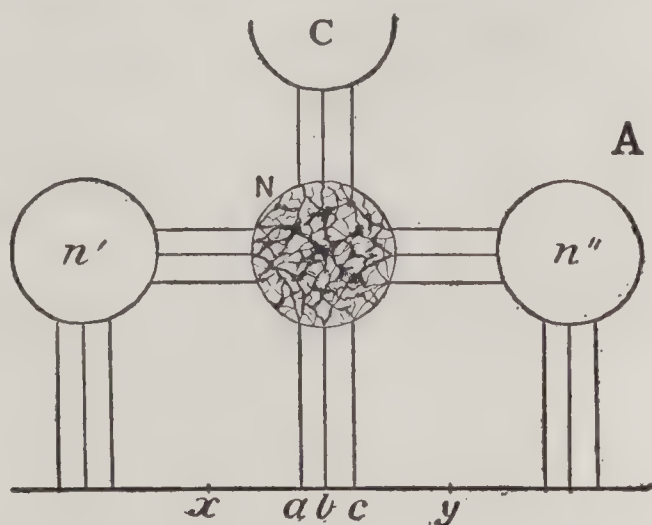


FIG. 39

A and B. Diagrams illustrating the process of nuclear division. $a b c$, filaments; n , nucleus; n', n'' , adjoining nuclei; C , central system.

surface where $a b c$ impinge, would travel inward to a central system and, potentially, also spread out laterally into the adjacent nuclei. Now, when the surface grows, say to double its size, in order to make room in the case of the retina, for more rods, it will be

necessary to double the threads $a\ b\ c$, and each of the new points, so as to be fully co-ordinated with the rest of the organism, must also be in as close connection not only with the central system but with the lateral nuclei as are $a\ b\ c$, the three points served by the threads.

We may perhaps assume that a branching of the fibrils $a\ b\ c$, would for a time meet the need of the expanding surface. But this branching may, for our purposes, be neglected inasmuch as, branching or no branching, a time would come when, in the interests of efficiency, the expansion of the surface has drawn the nuclei n' , n'' , so far apart that it would be necessary to have two new nuclei in the place which N alone filled before. We may then, for the purposes of the diagram, pass over the branching and consider how a second nucleus, with its three single threads running to the surface, might be produced so as to obtain the same number of nuclear connections, lateral and central, which in our diagram are assumed to be necessary to co-ordinate the new points on the surface with the rest of the body.

The theoretical problem before us now is to show in what way the division figures can be regarded as a device for dividing such nucleus as N and its connections with the surface so that new threads $a\ b\ c$, shall be produced, having relations with the surface, with one another, with the lateral nuclei and with the central system, exactly similar to those originally possessed by the undivided threads running to $a\ b\ c$.

The problem is a double one. In the matter of dividing the network, the diagram shows us somewhat unexpectedly that it is not necessary to split every thread longitudinally. An efficient method has been fore-

shadowed in our description of the division of the hypothetical unit, p. 17. All the threads running in or near the line joining the centres of the daughter chromidia simply have to be drawn out, only those in or near the plane of division have to split longitudinally. The process is essentially the same now though, instead of one chromidium, we have great multitudes massed together in a close reticular tangle and, instead of a single stellate system, we have a complicated network.

This comparison between the division processes of a unit and those of the developed protoplast is still further instructive, for there was no difficulty in separating the two halves of the unit, as we saw in our diagram, and we find what is apparently a return to the same simplicity of arrangement in the mitotic figure, with this same object, the moving apart of the two halves.

I begin, then, by assuming that a considerable amount of slipping is possible at the knots of the network. Our object being to obtain an arrangement as simple as that of the hypothetical unit, we must assume that this slipping takes place on so great a scale that all the knots of the network, including all those in the feltwork of what is called the nuclear membrane, run together into one central knot from which all the filaments, formerly arranged as a network now radiate in so many straight lines. The chromatin masses arrange themselves upon some of these filaments, typically, in the plane of division, while a small globule may or may not persist at the centre of the radiating filaments as the analogue of the original chromidial centre of the unit (see Fig. 39, B, p. 251).

The diagram has now changed from A to B. The

centre itself and the filaments running from the centre to the surface (in or near the plane of division) may now divide and split longitudinally or, if already divided and split, may now separate, apparently just as the two halves of the central chromidium of the unit

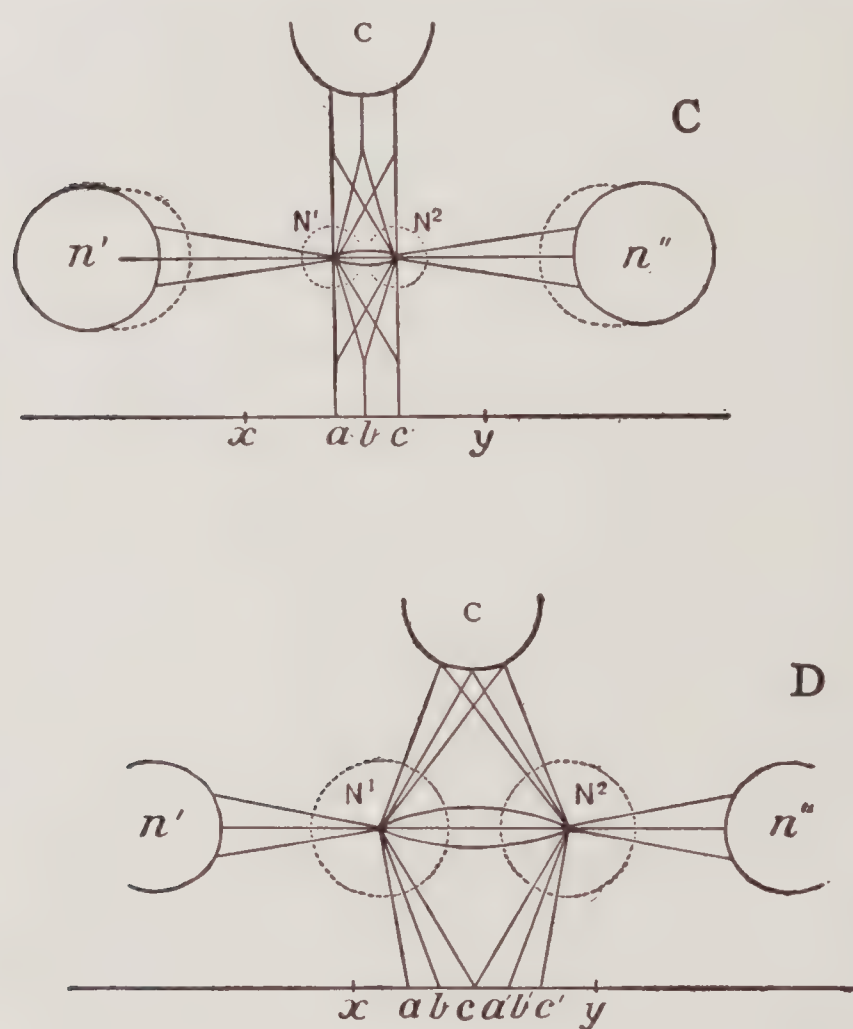


FIG. 39

C, D. Further diagrams illustrating the process of nuclear division. *a b c*, filaments; *n'*, *n''*, adjoining nuclei; *c*, central system.

separated, each carrying a stellate system away with it, and each of the two systems being the exact counterpart of the other. In the case of these more complicated organisms, in which every thread has its own special morphological and physiological value for the architecture and efficiency of the organism, we require

to assume a molecular arrangement which would allow the central knot to be divided into two knots, one representing the centre of one set of filaments and the other that of the other set. When these two knots move apart, we obtain the typical spindle figures of normal mitosis. (Fig. 39, C and D). The outermost or mantle fibres are due to the splitting or separating of the already split filaments running in or near the plane of division, while the axial fibres are those in or near the line joining the daughter centres which, as is obvious from the diagram, do not require to be split but merely to lengthen.

Any one familiar with the phenomena of mitosis cannot fail to recognise here all the essential features of that process: the disappearance of the nuclear membrane, the centrosome with its rays, the division of the same, so as to form the "asters" between which is stretched the spindle with mantle and axial strands, and the fact that nuclear division takes place, as a rule, parallel to the growing surface.

What the forces are that bring about mitosis, we no more know than we know what causes the chromidial unit to divide. It is of no small interest to note that the interpretation here given suggest that the complicated division of the nucleus has been gradually developed out of the simpler process of dividing the unit, and that division is now an inherited habit, an instinct to be ranked with other inherited vital processes. It is quite in accordance with our theory that the phenomena of mitosis should be explicable primarily as a division of the network, for that is the chief morphological element in the organism. It gives the form, and reproduction is the repetition of form. The movements and divisions of the chromatin are relatively

of secondary importance although, considering the closeness of the partnership between the linin threads and the chromatin, it would be going too far even to suggest the possibility of the chromatin being regarded merely as so much material.

On the other hand, it is quite clear that we must attribute the fact that this explanation has never yet been recognised to the circumstance that too much attention

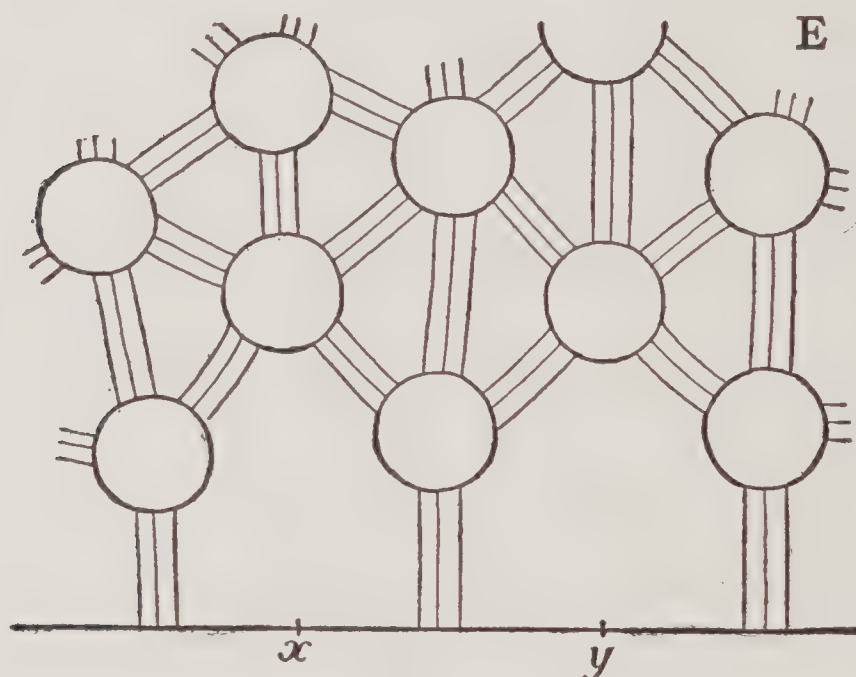


FIG. 39

Diagrams illustrating the process of nuclear division.
E. the resulting network.

has been given to the chromatin and too little to the thread system or reticulum on which the chromatin is suspended. The nearest approach to a recognition of the fact is, so far as I know, in a work by Kostanecki who showed that the division figure might be explained as due to a splitting of the thread system of the "cell." But the conclusion drawn, viz., that the object of the division figure was to divide the whole cell and not merely the chromatin, was still vague and not quite correct, for the division figure only splits the filaments in

or near the plane of division; the rest merely lengthen, and the network can thus stretch by having a mass of new filaments and meshes suddenly added by the splitting process.

This, however, is not the place to enter upon lengthy discussions; our business is to show, as briefly as possible, how our theory may be applied to difficult biological problems and to point out how all the known appearances of the network seem to establish the view that it and the chromatin are the two essential factors in organic life. With regard to the division figures, all I claim is that the protomitomic theory helps to explain them in their simplest and commonest form, as a device for dividing a network which must be assumed to return to its reticulate condition at the end of the process (Fig. 39, *E*).

Here, however, we run against an exception which is difficult to explain. It is by no means rare to find that the tips of the spindle, which are the centres of radiation, persist after the two nuclei have arrived at their normal reticular condition. We have, apparently, to believe that the point occupied by the centrosome, toward which all the nodes slip when the threads of the reticulum assume a radial arrangement, may be acquired as a point quite apart from the nucleus which is then, *pro tem*, merely an organ of the network upon the network and that its network can, in some way, dissolve by itself, its threads joining the radial system almost as a separate part of that system. Then, when the whole system has divided, that part of each daughter radial system which specially belongs to the nucleus resumes its network form for a brief period, leaving the rest of each network radially arranged. This apparently independent action of the nucleus is very remarkable,

though it cannot rightly be said to be any more difficult to understand than the simpler phases, for they all involve molecular re-arrangements which are beyond our powers to grasp. What we see in these cases of persistent asters may be compared to the permanent condition of our simple uniform network with the single chromidia at the nodes. Only, in the present case, in which we have reticular nuclei in place of complicated, it seems necessary for each nucleus (and only the nucleus), after having had its threads straightened out for the purposes of division, to return for a moment to its vesicular reticular condition before being again divided. We must refer this process to the physiological needs of the organism which the nuclei in their normal condition only can supply.

We once more find, in these cases of growth of the metaplast with rapid division and multiplication of the nuclei, a picture almost exactly parallel to that yielded by the growth of the simplest uniform network stage of protoplasm. The filaments of the network radiating from the chromidia lengthen and split—lengthen and split, perhaps rhythmically, gradually increasing the size of the whole and the number of the chromidia. The centrosomes or centres of the asters represent the dividing chromidia, while the radial systems are the filaments which repeatedly lengthen and split. This simple comparison is, however, in the case of the metaplasts, complicated by the nuclei being vesicles in which the mass of the chromatin is stored. The nuclei in this case are no longer the exact analogues of the chromidia, but are secondarily acquired organs which have also to be divided and which require, between each division, to recover their forms, take on their proper functions for a while and then undergo further division.

Let us now pass on to a very brief reference to the other part of growth in the biological sense, the multiplication of the individual to form families and colonies of individuals like himself.

A complicated metaplast might be diagrammatically represented as a continuous network ending all over the periphery as a fringe. The organs of the metaplast have, for the time, to be left out of account, and the whole thought of as a nerve reticulum, the threads of which all tend to come together in the brain.¹

Very early in its development, portions of the network ceased to grow and became enclosed; these were destined to reproduce the organism when the time came, *i.e.*, when its own development was complete. The energy of growth, being unable to increase or complicate the adult any further, is transferred to these two masses of the reticulum which were early set aside (see Fig. 47, p. 378).

The first thing to note is that these masses remained in fibrillar connection with the whole throughout. Their continued nutrition and their vitality, when they begin to develop, and the many subtle effects, mental and physical, they are known to have on the whole organism, seem to point to the fact that the connection is never severed, until the separate unicellular masses to which they give rise actually break away and find their way out of the organism. The cell doctrine alone is responsible for the suggestion that the growing eggs and sperm have no nervous or organic connection with the parent body, and the burden of proof lies with the upholders of that theory. For us, the continuity of the network remains complete until the

¹ An unfinished diagram illustrating these remarks was found among the author's papers.—Ed.

separation is actually proved by the ejection of the separated masses.

The eggs and sperm of the parents may thus be thought of as in direct connection with the parent until the moment of final rupture prior to ejection. I need hardly emphasise the relation of this view to many of the burning questions of the day, that is, to all those questions that turn upon the influence of the parent organism on the young; for instance, mental or physical traits acquired by the parent prior to reproduction may make themselves felt in the offspring forming, like buds, in the parental body.¹

Another kindred question at once arises and must be mentioned. In the passage of the detached egg toward the surface it may either receive a protective covering or shell on its way out, or else it may be arrested by a special muscular pouch, the uterus, from which it does not escape until it has run through some months of its developmental processes, *i.e.*, until it has acquired the bulk of its special generic characters. It is thus arrested only if it has the vitality of growth in it, a vitality acquired by having first met with and incorporated into itself a spermatozoon. The question I wish to put is: When it is thus seized by or else voluntarily stops in the uterus, do the ultimate fringes of its filaments actually unite with the fringe forming the lining of the uterus, so as to establish the organic continuity between the parent and the growing young, ruptured when the egg broke away? I am strongly inclined to believe that this is the case. No trace of

¹ In this connection, the part played by hormones (definite chemical substance which can be isolated) in the correlation of growth between various parts of the body and between parent and child must not be neglected.—ED.

such connection has yet been discovered, but this fact is of no great importance, considering that the fundamental filaments and the part they play as fringes, disguised in various ways, round the periphery of all organisms has not been recognised. But, like the epidermis (see pp. 159-167), where streams of matter pass along filaments to the surface, the wall of the uterus clearly supplies us with an organ along which matter could flow in fine streams on to the surface of any enclosed body, while, on the other hand, the fringe of the egg would supply this latter with so many passages of this same material throughout the organism.¹ But the question is, do these filaments join in any way so that the stream may be continuous, and the possibilities of direct nerve continuity be established? That filaments can join together we know from the facts of grafts of skin which become normally functional, and still more certainly from the restoration, after lesions, of nerve functions which, since they are known to be associated with the filaments of the axis cylinders, may be re-established by the union of such filaments across the site of the lesion.

Before continuing this subject of the possible channels of influence of the mother upon the development of her interuterine offspring, owing to the existence of direct organic continuity between their respective protomitomic networks, let us return for a moment to the eggs and the sperm.

We have described both of these as portions of the parental networks and therefore themselves networks.

¹ In the retina, matter is absorbed by the rods and conveyed through the whole organ apparently along special systems of filaments, so as to avoid interfering with the nerve stimuli passing along the rest of the radially arranged filaments (see Chap. XII).

This necessitates a new conception of the process of fertilisation which is usually thought of merely as the union of the male nucleus with the female nucleus, but must necessarily be much more than this, if the network is, as we have tried to show, pre-eminently of morphological significance. The network of a human egg need differ but little from the network of a dog's egg, but the difference, whatever it is, causes the net-

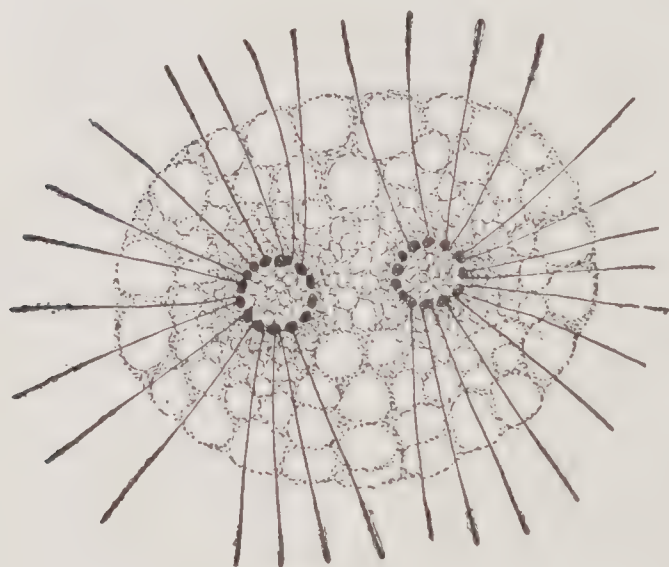


FIG. 40

Two individuals of *Actinophrys sol*, in conjugation. Conjugation is here seen to involve a union of the protomitotic networks (after Schaudinn, from Lang's *Vergleichende Anatomie* 2nd ed.).

work of the human egg to develop into an organism with the shape of a human being instead of into one like a dog. The point here is that these raw, undeveloped reproductive products are small portions of the networks of the same kind as those of the parents.

The fact that the reproductive products are in reality networks has not hitherto been recognised. The two kinds of networks are merely differently specialised, the egg having vast stores of nutritive matter upon its filaments which render them incapable of putting out any contractile energy for locomotion, while the spermatozoon is capable of almost the perfection of locomotion for such a minute organism, the great mass of its network being drawn out into a vibratile flagellum.

This view is to some extent confirmed by the discovery of Ballowitz that the flagellum, in this case, is, in reality, a bundle of fibrillæ, and it is further supported by the fact that this high degree of differentiation into male and female has not always existed, but is a secondary evolution from what is called the isogamous condition, when the conjugating organisms were of equal size, like those seen fusing together in Fig. 40. This makes it clear that conjugation has, from the first, been not only a doubling of the supply of chromatin, but also the union of two networks. What the exact nature of such a union may be we have no means of knowing; the filaments may actually fuse longitudinally.¹

Returning to our own immediate subject, viz., the witness borne by these phenomena of growth to the protomitotic theory, we come to the last question involved in the subject of growth, the fact that each growing organism repeats the details of structure of the parents. On this, also, I have little more to say than was said with reference to the constant repetition

¹ I am myself inclined to regard conjugation as an expression of hunger, the organisms in reality seizing each other as prey. It seems to me a likely hypothesis that the energy of growth and division arises from the absorption by each of half the other organism. Beyond this half neither can go but, instead of having mutually destroyed each other, the two now well-nourished halves form together a new organism with double the energy of an ordinary individual. This, to my mind, is a more probable hypothesis than that any part of the reticulum of the one is deliberately discarded in order to make room for a portion of the reticulum of the other. Such a deliberate exchange of definite parts would be difficult to imagine for, if the networks have the definite arrangement of the threads and nodes which we believe they must have, the eggs would always have to get rid of the same piece and the sperm always to have the corresponding piece to fit into its place. This preconcerted agreement between eggs and sperm is so highly improbable as to be inconceivable.

by each kind of Radiolarian of its own form of skeleton. The conception of a reticulum as the essential morphological basis of organisms seems to make heredity mechanically one degree more intelligible. The threads grow out on all sides, like branching trees fusing with one another according to definite plans, the plan of one egg differing from those of all other eggs except eggs of the same kind, and differing even then in the ultimate twigs, so that even within the same kind there is never exact similarity but always variation and the possibility of ever greater amounts of variation.

I, for one, see no possibility of accounting for all these ordered growths except by an appeal to a psychic force as accompanying the physical force. I will not say that the psychic is the dominant force, because there is so much in the variations of living forms that can be accounted for by the physical attractions and repulsions of the environment. The network can be shown to grow outward toward and into a suitable environment and to be repelled when the environment is repellent to it. The behaviour of the freshly cut willow twig is a classical example. That part of the network that is inserted in the ground always grows out into it as roots, while the part rising into the air forms leaves. These are the two forms to which the growing energies are in this case confined, and the response to the environment is instantaneous. The leaf tissue of the begonia is capable of acting in a similar manner; pegged to the ground it will send roots into the earth and a leaf stem into the air. It is to be noted that the growth of the fertilised egg is carefully shielded and protected from all outside impacts; no environmental attractions or repulsions can act upon it to prevent its network from growing according to the

acquired habit of networks of its kind. It is either shut up in a shell, with a sufficient amount of food, or else it stays in a pouch in the mother body and is fed through the walls of that pouch. As soon as its definite form has been assumed, and its organs and tissues have received the stamp of their characteristic specialisations so that they can begin to put their characteristic functions into play, the protection can be removed. Those functions being, as it were, factors of the positions of the organs of the body, themselves become a kind of environmental influence, keeping them from altering, and growth only adds to size and strength. The mystery lies in the fact that the network, thus shielded, can grow out and repeat the disposition of its threads and nodes just as the Radiolarian grows out and builds up, generation after generation, the same skeleton. In the Mammalia, as we shall see in Part III, there is a possibility of direct nerve influence between the parent and the embryo, but this would hardly make the mystery any less, because the nature of the nerve energy lies at the bottom of the whole matter, and if it can be produced by the parental network out of food, it can be produced directly by the network of the embryo. Given an association of a psychic element with physical frames, as illustrated in the mental processes in Man, we have to fall back upon it in the present case. Indeed, it is well known that we have ultimately to fall back upon some such force which we are unable to weigh or measure, but the certainty of whose actions can be relied upon in all problems dealing with the behavior of molecules and atoms.

Part II

THE COSMIC RHYTHM

CHAPTER XIV

RHYTHMIC EVOLUTION—INTRODUCTORY

“Yet one more rhythm, extremely slow in its action, may be traced in the phenomena of Life, contemplated under their most general aspect. The researches of palæontologists show that there have been going on, during the vast period of which our sedimentary rocks bear record, successive changes of organic forms. Species have appeared, become abundant, and then disappeared. Genera, at first constituted of but few species, have for a time gone on growing more multiform; and then have begun to decline in the number of their sub-divisions, leaving at last but one or two representatives, or none at all. During long epochs whole orders have thus arisen, culminated, and dwindled away. And even those wider divisions containing many orders have similarly undergone a gradual rise, a high tide, and a long continued ebb. The stalked Crinoidea, for example, which during the carboniferous era became abundant, have almost disappeared: only a single species being extant. Once a large family of molluscs, the Brachipoda have now become rare. The shelled Cephalopods, at one time dominant among the inhabitants of the ocean, both in number of forms and of individuals, are in our day nearly extinct. And after an “age of reptiles,” there has come an age in which reptiles have been in great measure supplanted by mammals. Whether these vast rises and falls of different kinds of life ever undergo anything approaching to repetitions (which they may possibly do in correspondence with those vast cycles of elevation and subsidence that produce continents and oceans) it is sufficiently clear that Life on the Earth has not progressed uniformly, but in immense undulations.”¹

ALTHOUGH the evolution of life on this planet has been a subject of research to workers innumerable, Herbert Spencer’s suggestion, embodied in the passage quoted above, has not yet, so far as I am aware, been

¹ *First Principles of a New System of Philosophy*, 2nd ed., p. 263.

seriously taken up. The idea thrown out is that life, when once it appeared, advanced in successive waves, these waves repeating one another in a way that shows them to be rhythmical.

This suggestion was not worked out by Herbert Spencer himself even when, in his *Principles of Biology*, he dealt as fully as was then possible with the laws of evolution, laying stress upon the impact of external forces and, among them, cosmical rhythms, such as those of seasons and tides, as examples of environmental changes to which the plastic forms assumed by living matter have necessarily to adapt themselves. There is no hint of any rhythmical advance in organic life. The idea seems, indeed, to have been still-born or rather to have flashed up momentarily and to have retreated again. Nor, during the fifty years of enthusiastic work devoted to the problem of evolution since Darwin and Wallace threw such brilliant light upon it in 1858, has any note been sounded even distantly suggesting periodicity in evolution. Most significant of all is the fact that Professor Haeckel of Jena has passed it over in silence. I mention him in particular because, when the works of Darwin and Spencer had raised evolution to the first rank of biological theories, it was Haeckel who deliberately set himself the tremendous task of reconstructing the whole chain of life, a task to which fifty years of his life have been devoted and during which almost every phase of organic life has come within his intellectual horizon, from questions of pure morphology to problems of religion. In his own summary of his evolutionary philosophy, we look in vain for any endorsement of Spencer's suggestion that evolution has been rhythmical.

It is not my purpose here to discuss in detail the passage that heads this chapter, nor to argue that the special instances adduced by its author do or do not point to such an evolutionary rhythm as he suggests, but rather to show in what way my own biological researches have convinced me of the existence of a progressive order in evolution. The series of waves that constitute the rhythm of which I have caught sight differ from any of those mentioned by Herbert Spencer, but they point unmistakably, I believe, to a rhythmical order such as he dimly apprehended.

The prevailing doctrine of organic evolution presents to us a vast stream of "cells" and "cell colonies" jostling and struggling with one another and with the adversities of their environments; some survive and the rest are killed off. According to a law of Natural Selection, only the fittest survive.

No one who has any knowledge of the facts doubts that this description of evolution is in the main correct, but it is far too vague. What are cells? and what are cell-colonies? What is the relation between them? are they all hurrying on in a stream?—toward what end? Whence did they come? Is it an independent rush?—a great fountain of life obeying its own inner laws? In face of these questions we are bewildered. There is no single point in the whole scheme that we can lay hold of as clearly defined and firm in the hand. It is true that a few general truths have been learned, but we do not yet know how far they are valid. The glimpses we obtain of underlying principles are too scanty. A few controlling, shaping and guiding forces have come to light, but only so far as they are negative. We understand the necessity of obtaining equilibrium,

the continual advance in heterogeneity as a necessary result of adjustments to new conditions and the elimination of the unfit. We know nothing of the forces that started and that still maintain the stream; nothing of the positive constructive laws (if there are any) which, given the underlying, driving force, have directed and still direct it toward higher forms. Is the direction straight, and the speed of progress uniform, or has the advance taken place in immense undulations, as Herbert Spencer suggested? We are far from having solved these problems or those still subtler ones in which the psychic element, which is somehow mixed up in the stream, is involved. We do not know whether the positive driving forces can be accounted for simply as complex expressions of chemical affinities and repulsions,—whether such purely physical forces are alone sufficient to account, as the so-called materialists assert, for the beauty and perfection of the adaptations of means to ends so abundantly revealed by life, or, whether, among the elemental forces of life, we must assume the co-operation of some psychic concomitant such as can certainly be recognised as playing an important part in the evolution of human societies to-day.

These are some of the problems that confront the present doctrine of organic evolution. We have passed the stage of triumph over the discovery and now, after fifty years, stand on the brink of the stream, conscious of a deepening ignorance. What we most need is to be able to read some clear and intelligible order into the stream; such an order, if we could only find it, would surely, in time, reveal to us some of the fundamental laws of life.

It is such an order, I venture to think, that has

gradually dawned upon my mind during twenty years spent in several distinct lines of biological research. While pursuing each of these separate paths, I seemed again and again to catch a glimpse of an evolutionary truth wider than any as yet apprehended, and these glimpses, when compared, were found to be merely different aspects of the same great law. Considered in the light of this law, the evolution of organic life breaks up into a series of periods, each advancing according to a fixed formula, and this periodical progression seems to me to claim a place among the vast cosmic rhythms which have in all ages fascinated the minds of philosophers.

The simplest way of introducing my subject to the reader seems to be to give, very briefly, certain results arrived at in my different lines of research.

During a prolonged study of the fine structure of the vertebrate retina,¹ I became convinced that the orthodox cell of biology cannot be regarded as the only important unit of organic structure. The cell, of course, exists, but it has been too crudely interpreted; many of its supposed fundamental characteristics are superficial phenomena, mere passing phases of physiological condition. The retina I found to be, essentially, not a layer of cells, but a filamentous network with nuclei suspended at the nodes where the filaments meet. The close examination of many other tissues, and of the simplest living organisms, confirmed in a remarkable manner the conclusions arrived at in connection with the retina. The universal presence

¹ The results of this study are fully given in six papers, "Studies in Retina," *Quart. Journ. Microsc. Science*, Vols. 43-47, and summarised in Part I, Chapter XII.

of the structure I had found in the retina and had called the "protomitomic network" was forced upon me. It thus became evident that protoplasm can be analysed into far finer elements than cells, elements of which the cell is merely one of the complex multiples. The simplest possible combination of these finest constant elements of all protoplasm seemed to yield a hypothetical unit of structure (called by me the "chromidial" unit) far smaller and simpler than the cell, a unit as elementary as any that we can at present discover, by means of which the very simplest organisms and those tissues admittedly difficult to analyse by the cell can be explained. The cell itself can be shown to have been built up by this unit and can be satisfactorily explained by it.

That the cell is not the only unit of organic structure was further impressed upon my mind when studying, for many years, the morphology of the stony Corals.¹ An endless variety of coral "stocks" passed before me in review, stocks made up of colonies that are built up by units, but not primarily by cells. The unit of structure of the coral colony is evidently not the cell but the polyp which, in its turn, can be shown to have been built up by cells. Not only the Corals but all Coelenterate colonies are built up of polyps, and so it seemed clear that, in the polyp, I had found a third unit of structure, the next higher, apparently to the cell.

Having thus come upon traces of three consecutive units of structure, the chromidial unit, the cell and the polyp or, as it will be called, later on, the gastræal unit, each in turn yielding new organisms of a type

¹ The writer was engaged for thirteen years in cataloguing the Corals in the Natural History Department of the British Museum.—Ed.

higher than its own, the idea naturally occurred to me that other higher units might be discoverable by the help of which we might be able to analyse the higher and more complicated organisms more satisfactorily than by the cell. It appeared, indeed, as if morphology might have been befogged by the universal custom of analysing all organisms by the cell alone, and that the progress of the science of life might have been retarded in consequence of our restricting ourselves almost entirely to accumulating facts and working with a conception of the cell which requires emendation. Reviewing animal forms with the object of finding traces of such units, I was able to reconstruct synthetically two more, the annelidan and the vertebrate, and thus to form a series of five distinct units of structure.

It was during my study of the stony Corals, also, that the *method* by which each unit in turn produced an organism of a higher type than its own, and introduced a new and higher period, became clear to me. Colony formation was seen not only to yield, by the Darwinian method of variation, an endless variety of forms which have gradually settled down to their various environments, but always, sooner or later, to have succeeded in producing a certain kind of colonial organism capable of starting a new period of organic life, all the organisms belonging to this period differing in *type* from those belonging to former periods. That colony formation has played a great part in evolution has, of course, been recognised before, but never, so far as I know, has this special kind of colony formation been accorded its right place as *the essential factor* in periodically raising organic life from one level to a higher one.

In the following chapters this periodical rise in the level of life will be traced step by step, from the simplest known living form up to Man, the highest organic unit, the unit by which the human colonies or societies of to-day have been built up. Each unit in turn and the period it starts will be discussed; it will be found that all the units have certain characteristics in common, characteristics indispensable to the work of producing a different type of organism. Each evolutionary period also, it will be found, can be described by the same formula, the processes in all cases being essentially the same, although the factors involved become increasingly complex.

Organic life is thus seen advancing out of the dim past upon a series of waves, each of which can be scanned in detail until we come to that one on which we ourselves, the organisms of to-day, and the human societies to which we belong are swept onward. Here we must necessarily pause, but can we doubt that the great organic rhythm which has brought life so far, will carry it on to still greater heights in the unknown future?

I am fully aware that there is no item in my scheme which may not be disputed; it includes many subjects that have been and still are keenly debated. I do not pretend that the evidence for it is in all respects satisfactory; it is incomplete and cumulative and much of it is indirect. But I offer it to my fellow biologists as the suggestion of a way in which the organic physical details which the present doctrine of evolution strings together in a more or less haphazard manner may be arranged in a rhythmical progression from the simple to the complex.

My scheme does not in any way discard the present

doctrine of descent, on the contrary it includes it; neither does it deny the cell doctrine, although it modifies it. It is chiefly in the stress it lays upon colony formation, a factor well known to the morphologist but never yet accorded its full value by the evolutionist, that it differs from all former schemes. Colony formation, by periodically complicating the approaches to harmony between organic life and its planetary environment brought about by natural selection, is shown to be the chief constructive factor in organic evolution,—the great force which starts period after period of a great evolutionary rhythm. In this way the modern view is transformed in an almost startling manner.

Coherence is one of the acknowledged tests of truth, especially in the case of events following one another according to fixed principles. I believe that my scheme will be found to be remarkably coherent and I hope that it may not only illuminate many of the dark places in modern biology, but may also be of some use to the psychologist and the sociologist.

CHAPTER XV

THE CELL DOCTRINE, ITS VALUE AND ITS INADEQUACY

LIFE, with all its startling phenomena is, at present, only known to us in association with a complicated substance for which the name of Protoplasm has been universally adopted.

From its purely physical side, protoplasm may be described as a very complex grouping of chemical elements, and the forces it displays are the resultant of the various chemical interactions of these elements. The living substance, so far as it is a substance, is a complex of chemical atoms so arranged that their natural forces may follow in the order necessary to produce the phenomena which, on the physical side, we know as Life. The substance is living only so long as this unique complex of forces is displayed; it is dead when this order is broken; between these two states, a condition of quiescence may be found which is called suspended animation.

Protoplasm has the power of assimilating the elements it needs in such order that the interaction between them maintains its essential life force, and it can get rid of the waste. The materials of protoplasm, therefore, are always new; that is a condition of its life; what remains through all time is the resulting force; it is this which never dies out. Protoplasm, further,

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grows at the expense of other substances and builds up the forms of life.

What the first complex of atoms and molecules was like, whose aggregate of chemical interactions represented, in its purely physical aspect, the vital force, we do not at present know. But above this original protoplasmic mass there are long series of forms varying to a marvellous degree in size, shape, and internal structure. The first of these to become an object of study to Man, who is but one of them, were naturally the larger forms that could be examined with the naked eye, and crude attempts were made to arrange these according to their external resemblances. When, later, living forms were compared with the remains of extinct forms found embedded in the rocks, a progressive degree of complexity was discovered in them, the simplest forms coming first and being succeeded by others with continually more complex organisation. This recognition could not long remain barren; it was bound to suggest that the forms of life had descended one from another by the known processes of reproduction, the younger forms undergoing changes by having to adapt themselves to changes in their environment. If so, all living forms could be arranged in definite sequences, the relation between the links being the natural relation of parents to offspring.

This theory of evolution, however, clashed with the generally accepted cosmogony of Moses, and consequently did not gain a wide hearing until, in the middle of last century, Darwin suggested a very simple and intelligible method by which the progressive differentiation might have been brought about. No one now doubts that all the forms of life on the planet to-day are the direct descendants of those that went before them.

Every one now knows that, as we go back to these earlier forms, we find ever greater simplicity until we arrive, theoretically, at one type of organism as simple as is compatible with the manifestation of the essential activities of life. This simplest of all organisms is rightly claimed as the common ancestor of all the forms of life that have yet appeared.

These momentous conclusions were not, however, based solely upon comparison and classification of the forms of life as whole organisms. It is doubtful whether these alone would ever have justified such a sweeping generalisation. They also largely rest upon a comparative study of the textures of the living organisms.

The first step in knowledge as to the structure or texture of the living substance must have been made long ago when it was found that the bodies of men and animals consist of flesh, bone, sinew, etc. At this stage it remained through ages until, within recent times, anatomy became a science, and the various tissues in complicated organisms, such as the mammalian body, were more closely studied and classified according to the differences they presented to touch and sight.

In the beginning of the nineteenth century, the compound microscope brought new worlds into view, not the least fascinating field for exploration being that presented by the various textures of the body. It was not long before a great generalisation was announced,¹ viz., that all these different textures, or tissues as they are now called, of the life substance ad-

¹ Schwann's *Mikroskopische Untersuchung über die Übereinstimmung in der Struktur und dem Wachsthum der Thiere und Pflanzen* was published in 1839.

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mitted of analysis on a common principle. Very minute “units of structure” had been discovered, and out of these, it was said, all tissues are built up. Each unit was thought of as *living* in living tissue, the life of the units causing the tissue to live, and the death of the units resulting in the death of the tissue. The differences between the tissues were accounted for by the different modifications and arrangements of the units. Impregnated with lime salts, and thus hardened, some units form, by their union into masses, the hard bones; others, drawn out into contractile threads and arranged into bands, form muscles; and, still further lengthened out for the conveyance of stimuli from one part of the body to the other, others become nerves, and so on.

Each of these units, or “vesicles” or, as they were ultimately but very infelicitously called, “cells” was therefore to be regarded as an elementary form of life, and this idea was strengthened by the fact that the microscope brought to view thousands of minute living things in every stagnant pool, creatures that were nothing but single “cells” living free and independent lives. As the “cell doctrine” developed, it was taught that the larger organisms, such as men, birds, reptiles, trees, grasses, were cell-states or cell-republics, their component units having to a great extent given up their freedom and become modified and specialised, some in this direction and some in that, in order to form organs each adapted for some specific function. The “cells” which were supposed to build us up were thought to enjoy all the advantages and to suffer all the disadvantages of belonging to a rigid but highly efficient community.

Thus, in the nineteenth century, the “cell” was

hailed as a revelation to man. It seemed possible to see, in its apparently least complicated free form, the *Amœba*, a survivor of the original undifferentiated masses through which life first appeared on the planet. What wonder, then, that the biology of the century consisted mainly in the study of the cell, as an organism big with promise of further revelations as to the organisation of life and as a valuable instrument for the analysis of the other forms of life? The cell doctrine presented us with small masses of living matter admitting of simpler analytical methods than could possibly be applied to large, complicated organisms, and also supplied us with a unit for the analysis of all the known forms since, if all were built up of cells, the series might be arranged in terms of cells. The cell has consequently been the object of unwearying research, as well in its free and independent state as when united to form those vast and highly differentiated "colonies," the bodies of animals and plants.

The cell doctrine undoubtedly helped greatly to endorse and strengthen the doctrine of evolution. The two were seen to support and illuminate each other. The cell doctrine supplied and explained the element of plasticity essential to the doctrine of evolution. Cells were units of structure by means of which all the varying forms could be analysed and the ascertained results of that analysis were recognised as being in harmony with the doctrine of evolution. This method of analysis has now, for over sixty years, carried the study of life from triumph to triumph, which is clear evidence that the cell doctrine, if not the whole truth, was a splendid approximation to it. All the forms of life and all the functions and diseases

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of life, with perhaps some puzzling exceptions which are too few to balance in the scale against the rest, can be described in terms of the cell. The doctrine has stood the test of all that energy of research which it inspired and now rests upon a mass of observation so vast and so certain that it is practically unassailable. All who grasp what this means will cordially agree with Professor Wilson in claiming for the cell theory that "no other biological generalisation, save only the theory of organic evolution, has brought so many apparently diverse phenomena under a common point of view or has accomplished more for the unification of knowledge. The cell theory must therefore be placed beside the evolution theory as one of the foundation stones of modern biology."¹

But, great and epoch making as the cell doctrine has been, no one in his most enthusiastic moments has claimed it as anything more than a stage in the gradual advance of our knowledge of life. It is by no means the final term in our analysis of organic structure. The very work which has been carried on by its aid has, for some time past, been demonstrating its inadequacy. It is easy enough to say and even to believe that all tissues are built up of cells, but the question of "how" is bound to come up. Some tissues appear to present no special difficulty for, to all appearances, they are simply aggregates of such units, but in the case of others it is difficult to imagine that the cell units that built them up were ever distinct, and all our attempts to analyse such tissues by the aid of cells alone are baffled. This secondary co-operation of cells is acknowledged to be a serious difficulty by the able

¹ *The Cell, in Development and Inheritance*, p. 1.

writer whose appreciation of the cell theory has just been quoted.¹

The solution of this difficulty has been sought by some in the developmental processes. An immense amount of research has been concentrated on the fine structure of the egg, its fertilisation and every stage of its development, in the hope of obtaining some clue to the cause and manner in which cells become associated into such a marvellous variety of tissues, but without success; these researches appear to contradict each other in a somewhat startling manner and have even raised, in minds capable of independent thought, a doubt as to whether cells, as units of structure, have any existence at all. Professor Sedgwick refers to the cell as "a kind of phantom which has always cropped up and blinded us to real organic structure."

In the evolutionary scheme the details of which are to be given in the following chapters the cell doctrine is not discarded, but modified. The cell is accepted as a unit of organic structure, but is shown to be not the only unit. By treating it as the second in an ascending series of units, many of the difficulties connected with the cell doctrine may, I believe, be met and removed, and the fine structure of the cell itself explained in a way hitherto unattempted.

It is to be hoped that, since the recognition of the cell as an instrument of analysis had been of such vast importance in the advancement of scientific biology during the last half century, the gain will be proportionately great in the immediate future if other units are recognised and as diligently applied to its still more accurate study.

¹ See Part I, pp. 81-84 where this subject is more fully discussed than it can be in this place.

CHAPTER XVI

EVOLUTIONARY PERIODS AND UNITS OF STRUCTURE

TWO great evolutionary periods and one unit of organic structure are recognised by the biology of to-day. The forms of life are grouped into a pre-cellular and a post-cellular period, the former comprising roughly all those organisms that are not typical cells or multiples of typical cells, the latter nucleated cells or their multiples. The cell is generally regarded not only as the unit of structure of the organisms that belong to the second period, but as *the primitive unit* of all living matter, the unit by the help of which all organisms can be analysed.

Until comparatively recently, the attention of biologists was claimed almost exclusively by post-cellular organisms. The forms classed as pre-cellular are mostly microscopic, some so minute, indeed, as to baffle the powers of all but the most perfect microscopic lenses, whereas, although some post-cellular organisms are microscopic, the great majority of them come within the range of unaided vision. Owing to this difference in visibility and also, no doubt, to the relative complexity of the forms composing the two groups, there has been a decided tendency to regard the pre-cellular period as insignificant as compared with the post-cellular, and to conclude that the cell may justly be regarded as the source of these

earlier forms, they being derived from it by processes of degeneration and fragmentation. But, of recent years, increased microscopic powers have brought precellular organisms more distinctly within the horizon of knowledge. An ever-increasing number of these minute forms of life are being revealed to us in all their marvellous variety, and the view of their origin from the cell, however plausible it may have been in the past, becomes more and more improbable. The myriads and ubiquity of the Microbes alone is such as to give them as clear an *a priori* right to be regarded as primitive organisms as the cell. Indeed, judging from the sequence which may be established on mere gradations of size and complexity, the Microbes, so far as their constitution can be made out, can justly claim to be more primitive than the cell.

I am not questioning that the cell is a unit of organic structure. No one can study tissues for any length of time under the microscope without having to admit this fact. The natural way out of the dilemma is to assume that it is not the only unit. We evidently need a simpler and more elementary unit with which to analyse all tissues and organisms not analysable by the cell, and to explain the cell itself and the pre-cellular period.¹

I must refer the reader to Chaps. I and XVIII for details of what I have called the "chromidial unit," the most elementary, I believe, at present discoverable. It is necessarily a hypothetical organism reconstructed by the aid of the three constant elements discoverable in protoplasm. What we here assume is that there

¹ See Part I, Chaps. I and XII, for an account of the researches into the minute structure of protoplasm which revealed this unit of structure.

is some such very elementary unit of organic structure which has as definite a morphological significance in its own way as the cell. All the arguments that are used in claiming that the cell is the primitive unit of structure justify us in starting with this still simpler unit which, further, has the great advantage of being a finer instrument of analysis for the investigation of the protoplasmic tissues than the cell could ever be, in that it takes us deeper into the nature of their textures, the cell being too complex for this purpose. I claim that some such unit produced all the pre-cellular organisms and, by combining into colonies which gradually became welded into new organic wholes built up, among other less successful organisms, the famous cell with which biologists usually start their record of life.

Let us now return for a moment, to the two evolutionary periods usually accepted as helping to explain the evolution of organic life. When we ask what separates these two distinct periods from one another, and how they differ, it becomes evident that the appearance of the cell in some way caused the break in continuity. There seems to be no transition from the pre-cellular to the post-cellular except through the cell. The advent of the cell thus marked an epoch in the evolutionary process and started a new evolutionary era.

But this answer is manifestly insufficient. It was not merely the appearance of the cell, but the fact that the cell built up colonies that caused the sudden break in the evolutionary stream. Had cells remained single, the pre-cellular stream would apparently have run smoothly through all time by the constant addition of minute structural variations, and it is doubtful whether organic life would ever have advanced in

complexity far beyond the level attained by many single cells. Indeed, any one who knows the elementary facts of biological science, will admit that it was colony-formation that enabled the cell to start the second and higher post-cellular epoch. It was this that suddenly flooded the world with hosts of new organisms to prey upon and be preyed upon by the organisms of the earlier pre-cellular period, as if they were two alien creations.

The evolutionary importance of the cell thus lies in the fact, not only that it was a very efficient unit of structure, but that it was able to build up colonies which, in their turn, were capable of specialisation into new and higher forms, thereby raising the level of complexity far higher than was possible to the smaller and simpler organisms of the pre-cellular period.

Here, then, is the first striking fact to which our preliminary survey and analysis of the kingdom of life calls attention. It is not new, but its significance has not yet been exhausted. Life progressed to a certain point until it produced the cell; on the production of the cell, it advanced by what appears, in retrospect, to have been a sudden leap. Not only was the cell a highly efficient organism in itself, as is clear from the fact that so many unicellular organisms still exist, specialised in thousands of different ways, but it had the power of multiplying indefinitely and forming colonies, which colonies have since become organisms specialised to numberless more and ever more complicated environments. For the specialisation of a large colony of cells as a whole must necessarily be able to reach a level of complexity higher than that which any single cell could possibly attain. We conclude, then, that, without the advent of the cell

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as a potential unit of structure, life would have remained at a comparatively low level, and that, by the cell and its capacity for forming colonies, life was raised from one level of complexity to a higher one.

Now, since the cell as a unit of structure has played such an important part in the evolution of organic life, raising its level of complexity and efficiency, is it not reasonable to ask whether this process has not taken place more than once in the course of evolution? We have shown that it is possible to account for the organisms of the pre-cellular period by referring them to a simpler unit of structure than the cell, a unit which, by colony-formation, produced the cell as a second unit of structure, and may not the cell, in the same way, that is by colony-formation, have produced a higher unit than itself, and these units others higher again, each new unit acting like the cell in raising the level of organic life? Such higher units might also prove more satisfactory than the cell for the analysis of the more complex organisms.

It is my purpose, in the following chapters, to trace the gradual evolution of animal life from the simplest to the most complex forms through five distinct evolutionary periods, each introduced by a unit resulting from the colony-formation of the unit of the preceding period. Each unit is thus of a higher type than the last, and the organisms belonging to each successive period are of a correspondingly higher type than those of the former period. The term evolutionary period will here be used in a very definite sense. Geological periods are, in a sense, evolutionary periods, but not in this sense. There are also other periods, such as the "reptilian period," etc., referred to by Herbert Spencer in the passage quoted on p. 269

as having suggested the possibility of a rhythmical development of life. But an evolutionary period in the sense in which the term will be used throughout this discussion is one started or introduced by a new unit of structure as the post-cellular period is recognised to have been started by the cell. A succession of such evolutionary periods, introduced by a series of colony-forming units has, I hope to show, played one of the most important parts in the evolution of organic life, raising it by a series of steps or leaps like that which raised the post-cellular period above the pre-cellular.

We shall find that almost all the known facts of morphology become evidence for our scheme the moment they can be shown to fall into line with such a sequence. The cell is a unit of structure simply because it falls into line. It is one of a series each link of which forms colonies, one of which, on becoming specialised, produces the next higher unit. These successive units carry life upward in a single continuous chain, each new link being of vastly greater organic complexity than the one that preceded it. But while each new unit has this chief function so far as evolution is concerned, it has other functions as well. Only one (or may be two)¹ of the specialised colonies it forms

¹ Only one single, main series of such units appears to have built up the concrete framework of organic life, though there are subsidiary series whose fates can generally be followed. Some of these appear to die out early, but one is known to have persisted side by side with the chief series, a persistence no doubt due to the fact that its organisms were able to tap a food supply unattainable by the organisms of the main series and to invade environments inaccessible to them. I refer to the vegetable series that has developed side by side with the animal. These two series which, in spite of occasional struggles, may and do effect serviceable interchanges, became in time indispensable to one another.

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can lead on to a new unit, but the rest take on a host of different specialisations so that, each time a unit has formed colonies, in addition to the production of a new form that shall raise the level of life, a host of organisms of the same level as the unit are suddenly intruded among all the lower and more stationary forms of the earlier periods. These intermingle and struggle with one another but have no power to make forward rushes; by degrees they settle down to conditions of equilibrium with their several environments, acquiring in this process a multiplicity of fine variations.

This series of units and the periods they introduce form the morphological framework of my whole scheme, as is evident from a glance at the diagram on p. 307 which, however, is primarily designed to illustrate another point.

A review of the animal kingdom reveals a series of forms which have had the power of building up colonies in the midst of vast numbers which possess no such power, but live their lives independently. The forms that now concern us are those that are usually, but not very happily, called “colonial organisms,” for it is a certain selection of these that can be linked together in an evolutionary chain such as I have described.

The Cell, the second unit of my series, gave rise by colony-formation to a vast number of organisms that have persisted and flourished throughout all subsequent ages; the chief of these are the Echinoderms, the Molluscs, and the Coelenterates. Of these, only the Coelenterates are “colonial” animals, and it is among them, therefore, that we have to seek for our third unit.

If one of the great coral stocks of the Madreporaria or stony Corals is examined, it is evident that it is made up of colonies of polyps, and it is the polyp, in its most primitive form, that is our third or gastræal unit. I have called it the "gastræal unit" because it is practically identical with the gastræa of Haeckel, which is regarded as the first morphological arrangement arrived at by the cell colonies. According to Haeckel's gastræa theory (which met with very wide acceptance) it was this particular arrangement that gave rise to all the higher forms of life. The fact that a primitive organism of this sort had existed seemed proved, not only by the existence of large groups of forms (the Coelenterates) of essentially this type, but also by the appearance, in the embryonic development of certain higher forms, of a "gastrula stage," this special arrangement of the cells resulting from the division of the egg. While this theory was a brilliant approximation to the truth, the gastræa is not, as at one time claimed, a stage through which the higher Metazoa have to pass in the way of ordinary descent. It, however, takes another place in evolution quite as high as that assigned to it by the famous German zoölogist in functioning as one of the single line of units of structure which succeeded in introducing a new evolutionary period. According to the view here enunciated, all the forms that can be traced by descent from the gastræal unit are still essentially of the same type as the gastræa.

The fourth unit of structure in our series (produced by the colony-formation of the last unit) is one short string of gastræal units, making a primitive Annelid,¹

¹ Comparable with the "Urannelid" of German authors.

an organism distinguished by immense muscular activity, by collateral symmetry and by freedom from all one-sided adaptation. This is one of the most efficient of animal forms and, as a successful unit, it has been able, by colony-formation, to build up a type of animal more complex than itself and of even greater efficiency. Among the annelidan colonies, we naturally find extraordinary variety in the lines of development for, the larger and the more complex the organism, the greater is the range of possible specialisations in adaptation to a wider range of environments.

Our fifth unit is one of the many highly complex specialisations of this annelidan period, one of the Vertebrate forms, a Simian or Anthropoid unit which, in its turn, built up great homogeneous social aggregates.

The reasons why these five organisms, the chromidial unit, the cell, the gastræal unit, the primitive annelid and the anthropoid ape seem to be the only ones that succeeded in directly helping forward the evolution of life, *i.e.*, why these were the chosen few destined to carry organic life on to the marvellous heights of complexity it has reached, will become clearer as we advance, but a few interesting points about these units may here be briefly enumerated:

- (1) They can be ranged in an ascending series.
- (2) They act as nodal points between which all the independent forms can find their places.
- (3) A certain resemblance can be traced between these successive forms.
- (4) They also stand in a definite architectural relationship, the higher having been built up of the lower, while all the independent forms that come be-

tween any two of them can be analysed in terms of the lower.

(5) This relationship is, in all cases, essentially the same however greatly, owing to the increasing complexity of the organism, the appearances may differ.¹

We shall find also that all the units possess certain characters in common and that it is these characters that seem to have led to their success. One of these is plasticity. Of all the thousands of cell forms admirably "fitted to survive" none that coated themselves over with hard substances could be used for evolutionary purposes. The cell which survived, not as itself, but as the builder up of a new and higher form of life was one unhampered by skeletal formation, one which remained plastic. And this is true of all the other units. The skeletal formations which enabled many of their contemporaries to survive fail to appear among them. They are, from first to last, forms specially sensitive to the environment, and showing great concentration of the forces of the organism. In the higher units, the muscular and nervous elements become specially developed for the most active possible life, with only so much skeletal formation as is necessary to render the muscles efficient or, here and there, to form plates to protect the vital parts.

Only a small selection of the colonial organisms combined these necessary characters. The stony Corals, for instance, though they developed thousands

¹ It is of course, this last point which constitutes the rhythmical character of the sequence. A series of colony-building forms showing striking characteristics in common and linked together by other organisms upon a fixed definite principle, is a rhythmical series, even though no numerical relationships can be made out between the factors composing the sequence.

of different and perhaps still differing forms of great intricacy and beauty and built up, with their skeletons, from the floors of tropical seas, continents now inhabited by higher forms of life, have no vital significance for the evolutionary advance of life. The new genera, species and varieties they produced have all remained corals, mainly because the polyps that formed the coral colonies acquired, in the process, a rigid skeleton which hampered them in their further development.¹ The Sponges afford another instance of a colonial organism which did not develop into an efficient unit of structure, and they may have been rendered stationary by the spicular skeleton which is nearly always present in them. Sponges, Corals, and many other colonial organisms thus drifted to one side of the main stream of evolution.

A series of units of structure such as I have here suggested would be of great assistance in analysing the forms of life and thus in enabling us to study them more scientifically. No one can deny that the power we possess of analysing a coral stock by means of two units of structure instead of one, *i.e.*, by both polyps and cells, helps us in deciding the exact position of the corals in the animal kingdom. It would be quite correct to call a coral stock a colony of cells, but that would not distinguish it from any other colony of cells such as a sea-urchin. Some more thorough analysis is wanted, and what could be more illuminating than to say that cells built up the polyps which again built up colonies and these last built up the coral stock? And what is true of this particular kind of organism

¹ See Part I, p. 295.

is true of all; they are all built up of all the units lower than the period in which they appear.

It seems to me that if only we had such a power of analysing organisms we should be a step nearer towards removing the reproach to biology that it is not an exact science. This it cannot be until we have some scientific method. Our present method of classifying is largely guesswork. The multiplication of the cell into "colonies" has resulted in forms so numerous and complex that, while we are safe in calling them "cell-colonies," we get no further towards a knowledge of biology than we should towards a knowledge of architecture by calling a cathedral a pile of bricks or stones. We might just as well attempt to analyse a great building by its bricks as describe any but the most rudimentary metazoan by its cells. The cell is useful for scientific classification only at and near the time of its appearance.

Let it once be established that all the forms of life have been built up by units which appeared in the world in definite order, and we shall at once have a series of elementary factors whereby, for the first time, the more complex organisms may be resolved into their real elements. Classification would then no longer rest upon chance resemblances between organs, but upon actual component elements.

CHAPTER XVII

COLONY-FORMATION AS AN ESSENTIAL FACTOR IN EVOLUTION

TWO kinds of variation are recognised in organic evolution, recognised, I mean, in the forms of life, as if they were things apart, living their lives upon the face of this planet and competing with one another as on a stage.

The first of these is that to which Darwin and Wallace appealed, viz., that organisms, for some reason, do continually vary in small structural details. According to the Darwinian doctrine, these slight variations are selected in the race for life; hence, in the process of time, organisms come to be differentiated into varieties, species, genera, and so on. This seems to be a very convincing kind of variation, and appears to explain the doctrine of species.

The second method of variation is connected with the universal phenomenon of growth, and is well illustrated in such organisms as the Protozoa and the Coelenterates. Each organism, when it has attained its full size, divides, so that where there was one organism there come to be two, which can separate and move apart. The variation here consists in the fact that, before separating, the two halves may divide again, the products of this division dividing once more and so on till the result is a number of individuals who cling

together as if they were all parts of a new mass, all being repetitions of the original organism. Now, such a mass of organisms may live side by side and remain a colony, the individuals of which yield some kind of advantage to one another. A colony built up in this way tends again to divide, and to form a second colony and what are called "stocks," such as occur both among sponges and corals.

But there is another fate that may overtake a colony. The different organisms that form it may flow together, the assimilating organs uniting to form one large assimilating organ for the whole mass, and the tissues which expended the forces of the component units may unite into one great system of tissues, and so on. The new colony that results may thus be a *new kind of organism*, with organs much more complex and powerful than any of the former separate organs, because built up of a large number of such single organs belonging to a number of formerly distinct organisms.

The first kind of colony-formation described results from a simple multiplication of the original units, which then function together, gaining something by mutuality and co-operation. The other kind of colony-formation results in an altogether new organisation, in which the organs are all new and more complicated: there are new assimilating organs and new organs of expenditure, etc., made up by the units that have run together to constitute this new kind of colony. It is in this latter sense that the term colony-formation will be used throughout this discussion.

Up to the present time, the method of change by the accumulation of slight variations has, strangely enough, been considered as the only one that has played any

part in the evolution of life; it is the only method that has been generally recognised as an essential factor in evolution.¹ The selection of the variations that are brought about naturally has been considered as the essential factor, no weight has been laid upon colony-formation. This is strange, because colony-formation of the second kind described is *by far the most striking way of modifying and altering an organism so as to build up a more efficient type*.

Informal recognition has, of course, been accorded to colony-formation as, for instance, in the case of the cell. It was recognised that it was only through colony-formation that the cell produced the Metazoa and that this was a very great step in evolutionary advance.

Many of the most interesting problems of colony-formation, also, have been exhaustively studied as, for instance, by Prof. Haeckel in his *Generelle Morphologie*, where he systematically discussed and analysed the forms assumed by organic life, and by Professor Perrier who, in *Les Animaux coloniales*, enumerated and described all the known forms due to that method of structure. But neither of these well-known biologists has seen in colony-formation anything more than a constructive principle, a principle of somewhat frequent occurrence but without special significance in the evolutionary scheme. Colonies are regarded by them merely as accidental knots in the evolutionary chain, of no value to the chain. I, on the contrary, believe, and hope to show, that they have played an essential part in the construction of the chain, and that it is only by recognising their true significance that we can gain even

¹ The view that evolution has been brought about mainly by the selection of large variations (mutations) has, of course, gained ground since this passage was written.—ED.

an approximate conception of what organic evolution has meant and now means.

The ordinary conception of evolution is of a great stream advancing more or less uniformly in a slow, stately manner by the production, under a number of known and unknown external and internal stimuli, of countless small variations. A struggle for life, incidentally with one another, but always with the environment, selects and accumulates those forms that can be turned to account, whether they appear to us useful or not. Now, we do not say that this is incorrect, but merely that it is only applicable in sections to evolution; it applies to each one of our single periods. The whole sweep of evolution has been made up of such periods. If, for instance, the organisms of the pre-cellular period had continued merely to produce vast multitudes of forms showing slight variations, this process could have gone on indefinitely without raising life to a higher level. It was necessary, if a higher level was to be reached, that one of these forms should produce the Cell which, by colony-formation, was able to start a new race of organisms which poured like a flood over the surface of the old stream as an alien and, for the most part, destroying invasion. Then, rushing over this, came other still higher organisms, each onrush of new and powerful colonies living upon the older, or ousting them from their environments. The cause of these sudden, periodic appearances of new and larger organisms was, in each case, colony-formation.

Evolution can no longer, I maintain, be regarded as a more or less uniform stream, for the chief cause of its advance has been the periodic multiplication of some

unit of structure to form new and stronger organisms to override all the rest. If we still like to regard it as a stream, we shall have to picture it as a current in layers or strata, increasing in speed and in the complexity of its components from below upward. I

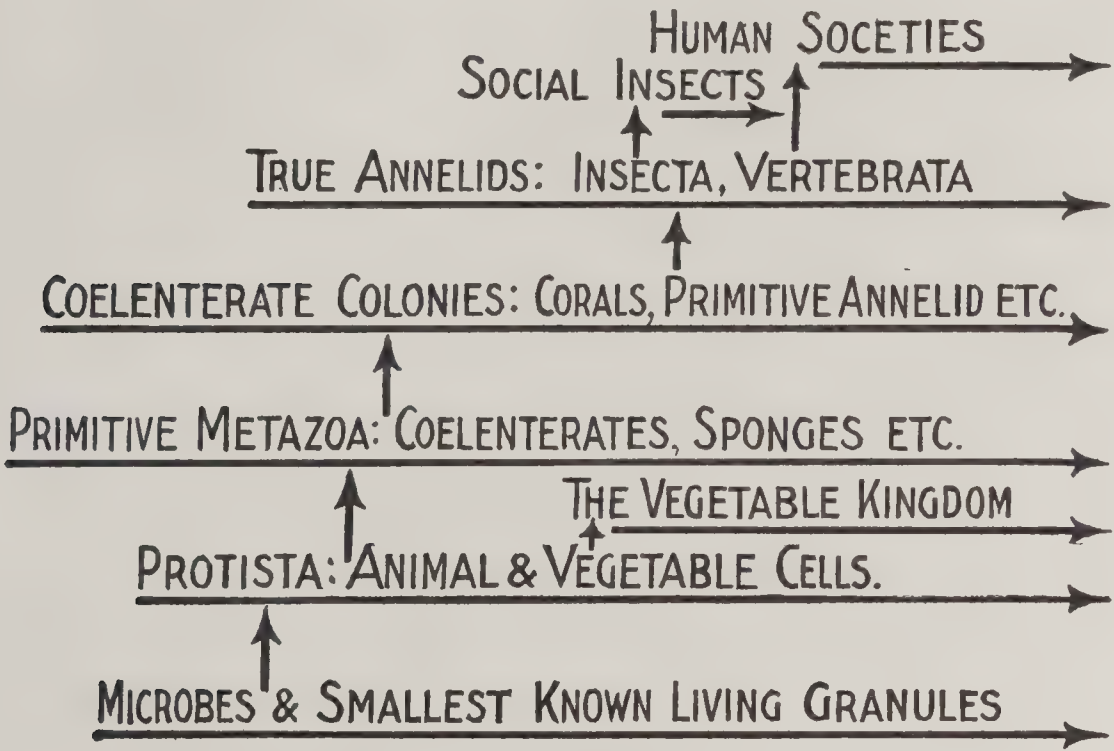


FIG. 41

Diagrammatic analysis of Organic Evolution into two series of factors, a horizontal series and a vertical series. The former represents the different phyla spreading over the face of the planet, actively equilibrating with their environments, but not, in so doing, rising in the scale of life. The latter represents colony formations which arise from some form of each phylum as a larger and more complex whole. These new "units," multiplying, invade newer and larger environments and thereby start new phyla.

prefer, however, to consider the whole as a chain of which the periods are the links.

The Darwinian doctrine that evolution has been brought about by the gradual accumulation of those variations that have been selected by Nature does not, consequently, apply to the raising of life vertically, but merely to what may be called its horizontal diffusion. Organic evolution may therefore be analysed

into two processes as in the accompanying diagram (Fig. 41), in which the Darwinian method of variation is represented by the horizontal lines and colony-formation by the vertical.

Along the horizontal lines, the offspring of each unit spreads over the face of the planet as one of the great phyla of living forms. The individuals jostle one another and penetrate into and become adapted to every environment in which life is possible for them. Each continues to vary so long as the environment varies, or remains stationary if the environment is so or, again, becomes extinct if the environment becomes impossible. It is to this series of horizontal planes of evolution, which comprise, in one aspect, the whole kingdom of life, that the laws of natural selection apply. It is a matter of accident whether the individual forms slightly rise or degenerate. In some of the horizontal lines there may be an appearance of rising, indeed, not an appearance only but a certain amount of definite rise which may play a great part in helping the more effective method of raising life obtained by colony-formation. Any such upward slope, however, may be counterbalanced by a downward slope elsewhere, representing the degeneration of forms through settling down to an environment in which the needs of life are too easily satisfied and the energies of the organism are consequently not kept up to the mark.

At right angles to these horizontal planes runs a different force of evolution, that of colony-formation. The upward advance is here started by the rapid multiplication of an organism on the lowest horizontal plane which produces an organic whole of a higher and more complex type than any before. The colonies of this new type then spread out over the planet by the

Darwinian method of variation, becoming ever more varied and together forming a second phylum. One of the organisms of this second phylum (the cell) repeats the process, and subsequently, on each higher plane one organism (sometimes apparently more than one) multiplies so as to produce a new type of organic whole, which then spreads out again horizontally. In this way organic life advances in complexity step by step.

Two other distinctions between the two evolutionary processes may here be pointed out. The Darwinian method of variation appears to be the more passive process, causing the spreading of living forms over the surface of the planet by passive adaptation to all the available environments. The living masses are the sport of their environment, their energies of response being called out, as it were, accidentally. Colony-formation, on the contrary, is essentially an active process.

It is one of the characteristics of living matter that it can not only protect itself against hostile attacks, but can itself advance to the attack, if such advance is repaid by the gain of any advantage. This interplay between the organism and its environment is what we call Life on its purely physical side and, by some means that have not yet been unravelled,¹ organisms become modified in shape so as to be always ready for their special environments. Now there are some environments that call forth all the vital energies of the living substance, the active reactions of which are enough to affect the shape of the mass and to turn it into a mechanism for special responses to special environmental impacts. The moment one of the protoplasmic

¹ I here purposely avoid plunging into the perennial controversy between Lamarckists and Neodarwinians.

masses produced by the ordinary ("horizontal") development multiplies by colony-formation, the organism, by the increase in its size, has to face the impacts of a much more extended and possibly more complicated environment. However complex the organism before it started colony-formation, it has, as a colony of similar units, to face the new and larger environment as a more or less homogeneous mass. Absolutely it must be more complex than any single one of its units, because it is composed of perhaps a hundred of such units. But relatively to the new environment it is more homogeneous and diffuse. The smaller individual unit had attained to some position of equilibrium with its much smaller environment, but the organisation of the new mass has, as it were, been dissolved, and has no special relation to the new, larger environment. It is as if the living substance repeatedly poured itself out over the surface of the planet in ever larger masses, to try its fate on a larger scale with the planetary environments. It is this, indeed, which gives us the clue to the action of colony-formation in the great drama of evolution. The living substance appeared in masses of definite size and, as the life which characterised them consisted entirely of their reactions with the planetary environments, which differ in countless ways in different parts and are even never the same for long in any one part, endless diversities arose as the result of the interplay between the "living" substance and the planetary surface. Conditions of equilibrium might, after a time, have been established in this way all over the globe, and every organism might then be classified according to the nature of its reactions. But this would mean that life would practically be at an end, so far as the possibility of further development was concerned.

Colony-formation comes to the rescue. The original living masses, instead of having to make the same response to the same kind of environmental impact through all eternity, acquire mechanisms which can be put to new uses. Larger masses are built up which actively invade the planetary environment, each new mass, on account of its size, now having to equilibrate with a larger and, usually, also a more complicated environment. This process, I believe, has taken place over and over again, adaptation to the surface of the globe alternating periodically with colony-formation which once more demands the adaptation of larger masses to larger and more complicated environments. The two processes have thus gone on hand in hand not only with each other but with the increasing differentiation of the earth's surface as the planet cooled down.

The other distinction that I would make between the two methods of variation is that the Darwinian method is more or less constant, while colony-formation bursts out intermittently.

This seems to throw light upon some of the problems that are left unsolved by the Darwinian doctrine, such as the transition from the pre-cellular to the post-cellular period, and the connection between the different phyla of the animal kingdom.

The view that the pre-cellular period is derived from the post-cellular is now discredited, some evolutionists, such as Professor Haeckel, being prepared to see in pre-cellular forms natural stages in the evolutionary process, leading up gradually to the cell. But what we have here to note is that the separation between the two epochs is sharp and distinct and the transition from the one to the other seems all to have passed through the cell. No ordinary development of vast numbers of

pre-cellular organisms, each evolving along its own lines could ever have brought about the post-cellular conditions; such a theory would imply the comparative stagnation of all but one form, viz., the cell, which alone carried on life to higher levels.

From such a hypothesis as this which, unsupported by any precedent and in view of the universality of variation, is simply desperate, we are saved by our theory of the periodic action of colony-formation in raising the level of life. Here we have a recognised case in which colony-formation has burst into the stream of unicellular organisms usually known as the Protozoa, and has produced a new and higher order of life, the Metazoa, thus beginning a new period. From the pre-cellular stream, advancing presumably by the normal process of the natural selection of minute structural variations, colonies suddenly shoot up and give rise to a second stream of larger and more complicated organisms; the two streams run on independently, yet each makes the environment more complicated for the other.

The phyla of the animal kingdom are those progressive streams of animal forms which can, with great plausibility, be arranged into families, genera, species, and varieties, inasmuch as they have some fundamental type of organisation in common, and their differences can be graded off into so many variations of that one type, and the latter may safely be regarded as due to the selection of small natural variations. The existence of the phyla, large and small, has been one of the chief evidences for the truth of the Darwinian hypothesis, that hypothesis being adequate to account for them. The Articulata may be taken as a good example of animal forms derived by gradual processes from the parapodial worms. The Echinoderms are another

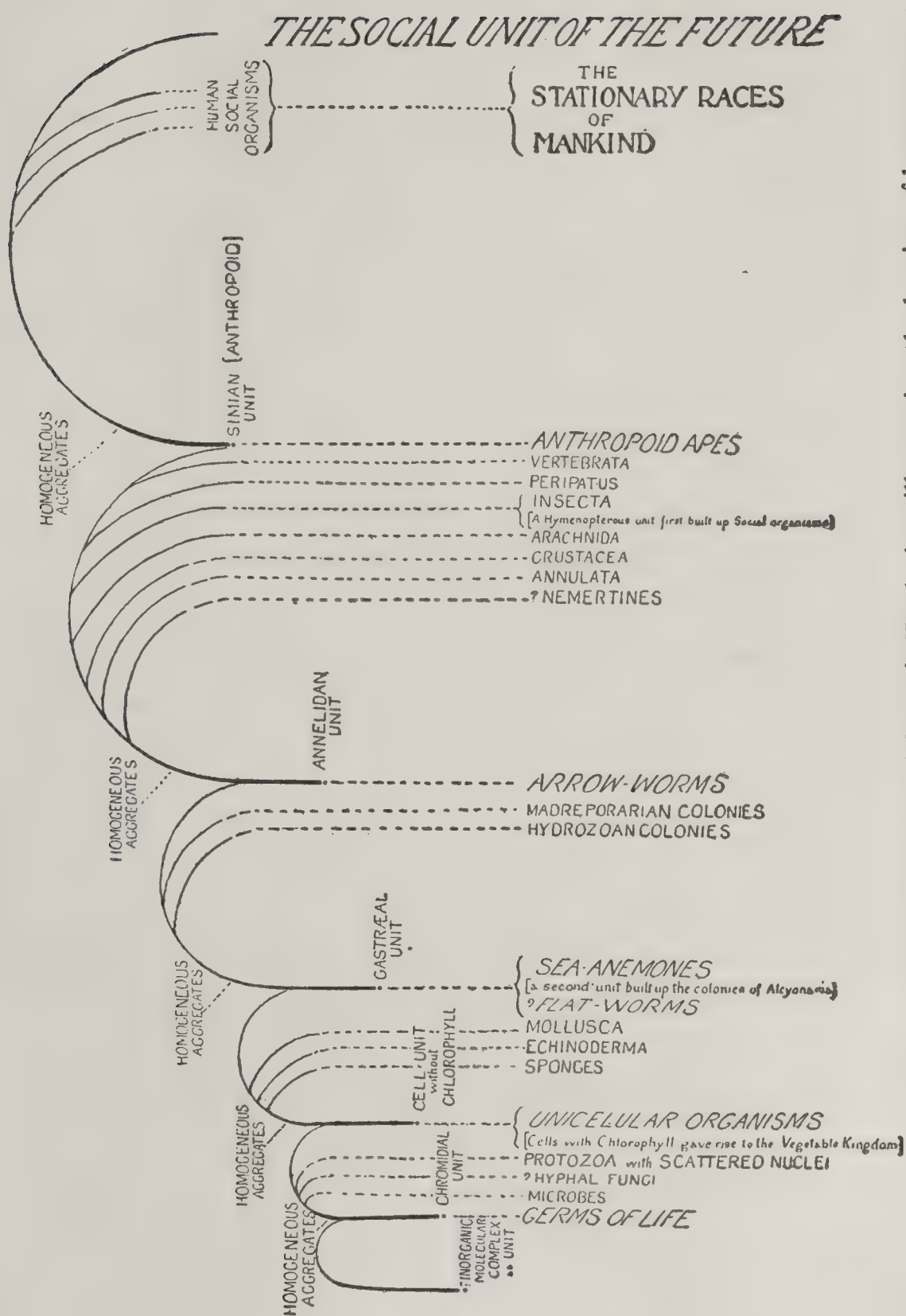


FIG. 42.—A general diagrammatic scheme of Organic Evolution, illustrating the lapsing of homogeneous colonies into heterogeneous organisms, showing how the introduction of colony-formation, as the chief factor in raising the level of organic complexity, results in an appearance of periodicity.

separate and distinct phylum which there is at present no means of connecting with the Articulata. The same is the case with the Mollusca, a very rich and variable phylum apparently springing up isolated and remaining isolated. Some method of uniting the roots of these great phyla has long been a desideratum among zoologists. I hope to show that colony-formation helps us to bridge over such gaps, and reveals the uniformity that underlies the diversity presented by organic life.

A second diagram (Fig. 42) compounded of the same two factors, the Darwinian method of variation and colony-formation, may help still further to illustrate the forces at work in the evolutionary process.

Herbert Spencer, in his *First Principles*, sums up the evolutionary process, whether of celestial bodies or of the forms of life, in a masterly formula, as "the lapsing of the homogeneous into the heterogeneous." Every student of Spencer, capable of expressing an opinion, has recognised this as a generalisation which bears the stamp of truth, but no one, so far as I know, has been able to apply it with success to organic life. It is faintly applicable to small sections of the evolutionary process in which we can see that a comparatively simple form of life has given rise to numbers of more specialised genera and species. Applied to the whole process of evolution, however, it fails, because, while we can see the myriads of heterogeneous organisms, we have no idea as yet of the homogeneity from which they have lapsed. What was that original living substance which, when first intruded on to the surface of the planet, began at once to adapt itself to its planetary environments with their rhythmical and other changes? What homogeneous, living matter was it which, through the interactions of its own forces with the external

forces of these environments, became physiologically differentiated and physiologically integrated into the organisms which we now recognise as the animal and vegetable kingdoms? Until we know this we cannot study its lapses into heterogeneity. We see the heterogeneous results but, as we look backward for their homogeneous origin, we can see nothing but the heterogeneous—always the heterogeneous, with some slight tendency towards the less heterogeneous, but never the homogeneous.

The value of a generalisation depends upon the degree of precision with which it illuminates the connections between the data with which it deals. We have here, in the Spencerian formula, a generalisation obviously true, but we cannot yet see how it can be made to apply to organic evolution as evolution is at present stated. It must be admitted, then, that, if the formula fits naturally and simply into our scheme, that fact alone tends to show that the latter more nearly expresses the truth than does the present doctrine.

Now, I claim that this Spencerian formula becomes perfectly applicable to evolution the moment we recognise the part which has been played by colony-formation. Each unit of structure has been, in a way, a new starting-point because its multiplication resulted in homogeneous colonies invariably lapsing into heterogeneity. The fact is, that the Spencerian formula does not apply to the whole scheme of evolution, but it is the formula of the evolutionary period, *i.e.*, of the link. The mistake we have made was to suppose that the lapse from homogeneity happened only once, and that the first homogeneous living substance has been lapsing until now. Our new evolutionary scheme shows this process to have taken place as many times as units of

structure have succeeded in producing new units. The colonies produced were naturally more truly homogeneous in the earlier stages when the units were comparatively simple. As they became more and more complex, the colonies were only homogeneous in the sense of being uniform aggregates of one and the same unit. By accepting the suggestion that units of structure have played the part we have assigned them in evolution, we obtain not one homogeneous mass but a succession of homogeneous masses.

Hitherto, in all our efforts to look backward to the origin of organic life, the view has been blocked by the Cell. This is, of course, from our point of view, significant enough, for the cell, being the first recognisable unit, might very naturally be mistaken for a starting point of evolution, whereas it is only the starting point of a period. But the fact remains that we have not been able to see behind the cell. It and its homogeneous colonies, lapsing into heterogeneity, have so completely filled the whole field of biology that we have seen no other periods, either earlier or later. We have even failed to see the other units which, sooner or later, took up the rôle of the cell, one after the other, and carried life to higher flights than were possible with the cell alone.

The Spencerian formula, applied to our periods, forces us to see that it is no longer upon a great mass of homogeneous living matter that attention must be concentrated as the hypothetical origin of life, but rather upon some living molecule which, by multiplying and building up colonies, produced the homogeneous masses required by the formula for the starting of the evolutionary process of lapsing into heterogeneity.

Here let us note that we are face to face with what

many think to be at the present moment the question of all questions for the biologist. What was the origin of the cell, and, in fact, of organic life? Upon these points the ordinary doctrine of evolution throws no light. It starts with the cell. Our doctrine, however, conforms far better with a philosophic conception of evolution in that it has no traceable beginning. It must go back to the beginnings of all things and all we can ever hope to do is to obtain some rational conception of protoplasm appearing on the horizon of planetary differentiations as one of the myriad atomic complexes which chemistry and physics have to unravel for us. We may legitimately claim that this is just the kind of beginning a philosopher might demand for any theory of organic evolution. It should be seen coming above the horizon, advancing by the same steps and evidently under the impulse of those same forces that carry it forward within the field of human vision.

We shall make a beginning towards establishing such an origin if we can show that there are good reasons for believing that the cell first appeared as a result of the colony-formation of some earlier unit far smaller and simpler than itself.

This conception of the origin of the cell is by no means new. An earlier hypothesis to this same effect will be described when we come to deal with the details. Here I must content myself with pointing out the significance of the fact that the cell, besides being a highly developed organism, presents, in addition to its colonial aggregates, an indefinite number of individuals showing variations of external form and of internal constitution, all of them being in comparatively speaking stable equilibrium with their several environments. This means, if it is legitimate to argue from the

Spencerian generalisation, that the cell and its many variations represent together the final term of that generalisation, viz., the condition of heterogeneity. If, therefore, the formula is true, as to which there is little doubt, such a condition of multitudes of heterogeneous cells implies some previous homogeneous mass, and that mass, we must now believe, was a colony built up by the multiplication of the unit which preceded the cell.

The diagram Fig. 42, p. 307, is an attempt to illustrate our evolutionary scheme in the light of the Spencerian formula. Each unit is represented as towering up by multiplication into its homogeneous aggregates, these then lapsing gradually into heterogeneity along their different lines of specialisation. And they lapse and lapse through all time, so far as they can survive the periodical influx of new and more powerful organisms produced by still higher units. In lapsing, they divide into families, genera, species, and varieties, each specialised for its normal environment, and adapting itself to the gradual changes of that environment. It is these downward streams of the forms of life for ever slowly modified to the fresh needs put upon them by external changes, it is these which make up all that, until now, has been recognised of the evolution of organic life. The new factor that alters the whole aspect of the problem is the recognition of colony-formation which, at the end of each period, seems to catch up one of the lapsing organisms and compel it to form new organisms on a higher level.

In this diagram, colony-formation is represented as having taken place rhythmically. This is in keeping with the suggestion of the opening chapter, and will be further evident when we come to set out the details of

the successive periods and find that these repeat one another closely enough to justify this view. At this stage of our argument, we only know that each period can be described by one and the same general formula.

The diagram shows a connected row of tree-like up-growths, whose branches droop and bend over. One of the drooping branches of each tree springs up again to form the next tree. The trees represent the sudden formation of colonies or homogeneous aggregates of some organism which acts as a unit. The drooping branches represent these homogeneous colonies settling down into adjustment with their respective environments. In doing so, they may have to struggle with one another and with some of the surviving organisms of earlier periods.

It must be borne in mind that the evolutionary chain is represented as coming out of the inorganic, and what we call period I may for all we know be period 500. Our period I is simply the first which it seems necessary as yet to reconstruct in idea, and therefore a convenient point to count from.

By way of contrast, let us recall the ordinary conception of a genealogical tree, the branches of which come, not from separate trunks, but from one another, all having one common origin from some single point, say from the middle of the top of the page. This point would represent the first living organism, which very few would dare to claim was the cell, although our systematised zoölogical knowledge usually starts with that organism. From this starting point a few branches would hang down and would again branch, and these again, until we have the known forms of life represented as the twigs on an ordinary genealogical tree hanging down the page like a creeper.

So far, one of these theories is as good as the other, and there is nothing which compels us to decide in favor of either in particular. The necessity for choosing only comes in when we study the material we have to work with. For the original living matter, whatever that was, has been no more free to choose paths of its own than is a crystal to take any shape it pleases. The laws governing its development may appear to us to be freer than those governing the growth of a crystal. But that means merely that they are more complex and have a wider range of possible variations; both alike are controlled by law. They can be interfered with from without, but from within they are inflexible. We owe all our diversity of life to the unceasing workings of these inner laws of the life substance, acting upon and being acted upon by the external forces of a very variable environment.

This description of life will, we know, give offence to some as being too materialistic. It will be said that in such a purely physical view of life there is no room for the spirit and soul of Man. I have no intention of shirking the question. It will be dealt with later on when we have to face the subtler problems of life. At present, we are dealing simply with the physical framework of evolution which, like the physical framework of an individual, has been built up according to physical laws.

Referring solely to this physical framework of evolution, it seems evident that, before we can judge as to which of the two schemes of evolution before us is the more probable, the essential characters of the living substance itself have to be defined.

Now, according to either theory, we shall not be far wrong if we regard the original living matter as one of the myriads of "fortuitous" chemical combinations

of the elements which built up the planet. Since all were in violent commotion until the earth had cooled down at the surface, none would be perfectly stable until that cooling had reached the absolute zero. But the particular combination of elements which started organic evolution seems to have been distinguished by certain very remarkable characters, remarkable, that is, when seen alone, but probably, when compared with those of other combinations, of which we yet have no precise knowledge, not specially surprising, for the dying forces of the once fiery planet were retreating into these smaller combinations. Into the mysteries of molecular physics science is still trying to penetrate. The recent discovery of radium has thrown open a new door through which physicists are now peering, endeavoring to find clues to the difficult and hitherto undreamed-of problems which are presenting themselves.

The long and close study which has been given to the life-substance has as yet yielded us no certain insight into the subtler molecular forces underlying and guiding its processes. We are able, nevertheless, to formulate certain conclusions as to some of its more obvious general characters. We can, for instance, safely assert that the living substance differs from a crystal in that the latter adds new matter to itself externally, and in this way grows into shapes the fundamental principles of which are fixed, while in living substances, new material is taken from without and is worked up into the mass.

But this in no way exhausts the differences. The living substance is far more active for, although it may appear stationary, its internal constitution is such that it may be termed a "stationary vortex."¹ It not only

¹ This term, originally applied to the Crayfish by Huxley, is applicable to any living organism.

takes in new matter, but it discards waste; that is, matters whose reactions are exhausted and can no longer be of any service to the maintenance of the energy of the molecular complex. This vortex grows only so long as the new material taken in exceeds the waste. It diminishes when the waste exceeds the new matter, and, as we say of such a dwindling organism, it dies. All this is simple enough. But now we come to the most important point of our argument and probably the most striking character of living substance, differentiating it not only from crystals but from all other elementary chemical combinations. I claim that the phenomena of life show clearly that there must normally be some maximum size beyond which the living molecule cannot grow and that, on reaching this size, some mechanical necessity of its inner constitution forces it to divide into two normally equal halves. These halves then grow to their maximum size and again divide, and so on.

I do not propose here to deduce the evidence for this repeated division. "Spontaneous division" is such a common phenomenon in living organisms that its existence as a fact of life needs no proof. It must have started somewhere and at some time and its universality compels us to assume that it is necessitated by the fundamental constitution of the original protoplasmic molecule, and that it goes through all life *ab initio*. The evidence for this conclusion will be gradually accumulated as we advance and will be in a manner summed up in a chapter on the vital forces.¹

One more fundamental characteristic of the living matter must be mentioned in connection with this phenomenon of equal division. Each half repeats

¹ See Chapter XXIII.

exactly the form and constitution of the original whole, and further, if any organic aggregate or colony of such wholes throws off any of the halves of its units for them to grow free of the aggregate, each of the halves so thrown off will reproduce as nearly as external forces will allow (first by growth of the half, and then by repeated division of the completed unit) the exact form of the parent organic aggregate from which it was discharged. This is the law of heredity. We shall have to discuss it again later on, in order to show that some, at least, of the mysteries in which it is shrouded, are due to a failure to recognise the factors. But, however that may be, the forces which govern this marvellous power of repetition are as unknown as are those of the stationary vortex itself.

Now, these are fundamental facts or characteristics of "living" matter, unless recent researches of which I am unaware have modified them. With these at our command I trust to be able to show that, without the periodic intervention of colony-formation, evolution could never have lifted organic life to the level it has reached. That is, the single branching tree doctrine of evolution has to give way to one showing distinct periods.

The inadequacy of the ordinary doctrine has, in fact, long been apparent. A very brief sketch of it will suffice. It assumes that masses of living matter in its elementary condition appeared on the surface of the planet. These masses naturally became subjected to all the impacts of an ever-varying and often rhythmically varying environment. The consequent interactions would necessarily compel the living masses to become progressively more heterogeneous through all time, growing more and more unlike as they settled down

to different and perpetually differing environments. At the same time they also became more and more complex as they learnt gradually to adjust themselves to the minuter complexities of these environments.

This process, it is thought, has been going on continuously through all the geological ages since the living substance first appeared. All the forms of life are, according to some, to be accounted for by this perpetual adjustment, and by this alone. Others, however, would postulate additional known and unknown causes of variation besides the mere necessities of adjustment. Among known causes which are thought to have played an important part in the production of morphological variations, are the differences started in the young from having two parents who must have differed from one another. Of unknown causes we note the recent appeal to "Sports," that is, to the occasional and inexplicable appearance of what is meant by the popular word "Freaks."

I would not deny the existence of variation owing to the fact that each individual has two parents, nor, again, that variations may occasionally appear spontaneously; that is, from within, according to laws as yet inexplicable. But our diagram proclaims two great factors: (1) The formation of homogeneous colonies; (2) the lapsing of these colonies in adaptation to environments. As compared with these, all other factors are quite subsidiary. The prevailing doctrine of evolution overlooks the periodic colony-formation and takes into consideration only the second of these factors, consequently the chief question has been whether the lapsings in adjustments to environment that have taken place on so vast a scale

were mechanical and direct (Lamarck), or were the result of the selection by the environment of those spontaneous variations which happened to be favorable for the environments in which they appeared (Darwin). We have to choose, therefore, between two schemes, one which represents life as advancing through all time like a tree or creeper by some continuous and uninterrupted process of gradual adjustment to the environment, and another into which periodic colony-formation enters as an essential factor.

Among the objections to the current doctrine is that raised by the physicists who tell us that the age of the habitable world, according to their calculations, will not give us time enough to build up, say, a human being from a protozoan, by any gradual and continuous adjustment by minute variations.¹ Another objection is that of the experimental students in variations and their inheritance, who hold out little hope of explaining the enormous advance in complexity seen in organic evolution by any principle of accumulations of small variations. For, among other points, it is found that though induced variations may be inherited for a certain time, there is always a tendency for the form to revert to the normal. These two objections, the time and the inheritance difficulties, are not, by any means, the fundamental objections, though they arise when we have to deal with the evolution of Man from a single cell. No one who knows the most elementary facts of biology would dream of stating that Man has been slowly evolved from a cell by the gradual accumulation of minute variations, caused either by direct

¹ This objection is not now of such importance, since the discovery of radium has enabled the physicists to allow a much longer period for the evolution of the habitable globe.—ED.

adaptation to environmental changes or by conjugation. Every zoologist knows that the first process in the evolution of Man, so far as the cell was concerned, was the production of a cell-colony.

The cell cannot be considered as Man's ancestor in the ordinary sense, but merely as one of the units of structure which helped to build up his first real ancestor. Here, then, we are met at once, in the elementary facts of zoology, by a principle that cuts quite across the ordinary scheme; a new principle that at once assigns to regular descent with accumulation of small variations a less exclusive place as a factor in evolution. The new principle by no means negatives the old recognised factors. We want them all, but it is easy to see that, for the actual *raising* of the level of complexity, we must look to this new factor and recognise the enormous influence which colony-building has had in producing the final result.

But we can now go still deeper than this. For, if my account of the fundamental characters of the living substances is correct, especially if it is true that the living molecule cannot normally grow beyond a certain maximum without dividing, then the only possibility of any organism growing beyond some more or less definite limit is colony-formation. Why it should be so we do not know, but we shall see that this law seems, with some qualifications, to hold throughout, and is illustrated in one way or another by all organisms, however large and complicated, as soon as they become integrated into organic wholes. It may be possible, so far as larger forms are concerned, to co-ordinate this necessity with the development of organisms as nervous systems or instruments of the "psyche"¹ but,

¹ See p. 437.

physically and in the first case, it must be referred to some peculiarity of molecular constitution which we are unable mentally to reconstruct.

Now, in the face of a growth limit, it is not difficult to show that, without colony-formation, evolutionary progress must sooner or later come to an end. Increase in complexity or, in the language of Spencer, heterogeneity is essential in such progress. But this surely must come to an end if growth in size is limited, for under those conditions variation can only be intensive. A limited number of parts adjusted to a limited number of environmental reactions cannot vary for ever. Even though an organism were to change its environment repeatedly by rapid locomotion, it would still, sooner or later, exhaust the possible changes. Here, also, we can appeal to the law of heredity which would effectually hamper variability. Indeed, it is not impossible that the law of growth limit and the law of heredity are but different aspects of the same fundamental fact,—the persistence of the fundamental molecular vortices which make up the living substance both as to size and shape.

In larger forms, there may be some secondary relaxation as to size, but that a growth limit exists, which is only rarely exceeded and then never to any great extent, is common knowledge. The relaxation, in large organisms, may be due to the fact that, instead of dealing with the first living molecule of the smallest number of parts, we are dealing with organisms which are vast colonies built up by myriads of such molecules. It obviously might become a matter of indifference how many units, within certain limits, go to make up a colony.

I admit that this subject is somewhat involved and we

cannot do better here than illustrate and expand it by known examples. The cell is not a single molecule of the living matter, but a specialised organism, built up of vast numbers of molecules, the exact number being a matter of indifference. Hence, within limits, the cell varies in size. But note, now, that this growth in size does not, except in a very superficial manner, increase its degree of complexity; its fundamental structure is the same; it still remains a cell. If it has to produce larger organisms on any higher plane, it can only do so by colony-formation.

A much more striking example is afforded by the Molluscs. It would be difficult to conceive of any organisms produced by the cell-period, *i.e.*, out of cell-colonies, more complex or showing more startling size-variations. But the Molluscs are always Molluscs, and there is no form of variation which can change them into anything else. This is a startling fact. Neither the Ammonites of old, nor the monstrous forms of Octopus and Squid occasionally met with in the seas to-day, were or are anything more than mere variations of themselves; they will remain such and nothing more as long as the world lasts.

The giant Cephalopod is far larger and far more complex than the primitive Mollusc which may have been no larger than a pea or bean. This difference in size and complexity between the lower and the higher forms produced by descent with accumulations of small variations may easily, at first sight, be regarded as quite as great as that between the gastræa and Man. It obviously represents an evolutionary advance without colony-formation, but it is not an advance in the sense of raising the level of life. A complex Cephalopod

may have been able to multiply the number of embryonic cells resulting from the early growth (*i.e.*, colony-formation) of its egg, and thus produce continually larger offspring, and may even, as an adult, continue to grow. But it will never be able to escape the burden of heredity; it will have the same type of organisation through all time. It will never cease to be a Mollusc. Though its size is larger, and it will be able to confront larger elements of the environment, that environment will remain practically what it was for its smallest cephalopod ancestor.

The same holds for all organisms. Though the law limiting the growth of any established organic whole may, in the course of long periods, be gradually relaxed, and though small surface variations may become very considerable, yet the fundamental, or what I have elsewhere frequently termed the "essential morphology" of the organism remains fixed.¹

We are thus definitely driven to the conclusion that fundamental changes of constitution, raising what we have called the "level of life" by altering and improving the ground plan can only be brought about by colony-formation. The cell produces the Mollusc by colony-formation. But the Mollusc, being unable to produce a successful colony of Molluscs, is still a Mollusc and, in spite of a thousand superficial disguises, could never be anything but a Mollusc. The cell also

¹ I would like here to call attention to the fact that we must avoid all connection with or confusion between the method of variation by colony-formation and that by small structural variations due to the perpetual interactions of the organism with the medium. By no possibility can such changes be regarded as belonging to the same category as colony-formation, which is essentially the multiplication of individuals within one and the same medium though, in the colony-formation with which we are specially dealing, the individuals are organically united so as to form one large homogeneous organism.

produced the polyp or gastræa, which, unlike the Mollusc, proved able to produce new and successful colonies, such as the Annellida. It raised up organs of higher complexity than itself by multiplying itself and by the multiplication of its organs which, fused together into organs that were larger and capable of greater variation and also somewhat differently disposed in the new wholes, caused those wholes to be organisms of a different and higher type.

This new description of evolution has at least two advantages over the old. The time difficulty raised by the physicists against the ordinary doctrine of evolution by descent vanishes at once. The slow accumulation of minute variations gives place to the sudden periodic raisings of the level of life by colony-formation. Secondly, the burden of heredity is relieved. The older doctrine by descent assumed that the accumulating burden was carried through all the long period of evolution, what is useless being discarded by some quite inexplicable process, inexplicable in the face of the rigidity with which organisms are compelled to retain their types through countless ages. But this burden is, according to my view, periodically thrown off, for the new organisms, lapsing from new colonies, start afresh. The real sphere of heredity seems to be mainly confined within the generations of the lapsing organisms of each period. It piles up its burdens afresh with the showers of organisms produced in every new period.

How rigidly heredity acts may perhaps be gathered from the observations of those who experiment with variations and find a constant tendency to revert to the normal. But, in all these cases, supposed to exemplify the force of heredity, we shall never arrive at any intelligent conclusion unless we keep two factors in mind:

the persistence of the living vortex, and the environment within which and, I believe, in conjunction with which it has its being. If the environment is changed, sooner or later the vortex must change or else be stopped by the friction. I would claim, then, that normal variations, are for the most part, attempts at adjustments to some change in the environment. When variations are induced artificially, it is usually the environment which has been tampered with. Cross-fertilisation would slightly alter the inner forces of the organism, but chemical or physical stimuli alter the environment. But if the organism is complex, one may be sure that its environmental factors are also very numerous and complex. And the tendency to revert, so often complained of, would seem to indicate that our interferences either with the inner or outer factors have been insufficient to upset for long an equilibrium established through ages between an intricate organism and an intricate environment. The normal equilibrium is re-established or, in other words, the organism reverts.

The doctrine of evolution by descent alone, *i.e.*, through the inheritance of vast numbers of minute variations, brought about by known and unknown causes, is thus, I believe, unable to account for the facts of evolution; the alternative scheme here propounded, which takes the growth limitation into account and over-rides it by repeated colony-formation, which latter also means a repeated bursting through the trammels of heredity, seems to me to offer a more exact and satisfactory solution of the problem of evolution.

CHAPTER XVIII

THE EARLIEST RECOGNISABLE EVOLUTIONARY PERIOD, THAT OF THE CHROMIDIAL UNIT

I CANNOT describe the exact details of any period actually emerging from the inorganic periods. Judging, however, from what we know of the organic periods, and from the fact that these latter repeat each other so exactly as to leave no doubt of their rhythmic character, I feel confidence in affirming that organic life arose out of the inorganic by essentially similar process, *i.e.*, by the clinging of complex molecules, as mere chemical compounds, to one another. Such clinging would produce homogeneous masses which then lapsed into heterogeneity, having to seek equilibrium with an indefinite number of different planetary environments. Some might at once settle down to equilibrium, some would perish, others fall upon variable environments and gradually acquire the power of maintaining an equilibrium, slight changes of the environment being met by slight changes in the new compound. As soon as this interplay between the compound and its medium is attained, we have the beginnings of Life.

We may be reminded that this interplay is taking place between every object in the universe and its surroundings. Even mountains dissolve away under the action of wind and rain; nothing can for ever resist

change. Then wherein does a living form differ from all these other changing forms? In this fact that, in the compound which we call "living," the molecules build themselves up again as fast as they are broken down. This process of building up can, of course, only take place in a medium from which the material required can be obtained. Hence there are only limited environments in which life can be maintained and, in the nature of the case, since each living molecule has to build itself up by contact with the medium, the first beginnings of life must have taken place in molecules. The primitive molecule must have had its own organisation, but what that was is a problem dipping away into the unknown, far out of the range of the present attainments of the chemists.

We do not yet call this molecular organisation the life of the molecule, but that is probably what we are soon coming to. For let us suppose that a number of these molecules cling together, and then have to learn to carry on the interchange with the medium as a mass instead of each one for itself. The whole process becomes more complicated. The internal forces of the mass are multiplied by the number of individuals it contains and, at the same time, some exchange between the individuals must take place; those on the outside of the mass have to bear the brunt of the conflict with the medium and have to hand on to those within the mass what they have acquired, at the same time not only parting with what they themselves have to give up to the medium, but passing out what those internally placed have to get rid of. Now it is this more complex organisation which we begin to call organic and the interchange with the environment on this larger scale is what we call Life.

Organic life, I suggest, rose out of the inorganic in this way, but by how many processes of colony-formation I cannot say. When first we feel our feet,

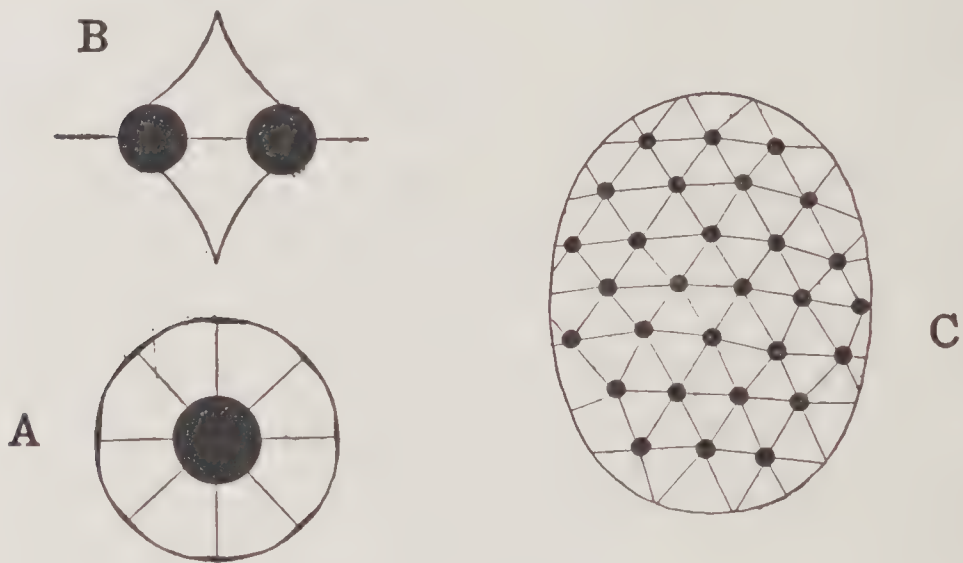


FIG. 43

- A. The Chromidial Unit as a mass of chromatin with linin threads which are at the same time nervous, contractile, and synthetic. The waste matters of its chemical reactions, carried out from the central mass along the linin threads, are deposited as a pellicle at the surface of the fluid mass in which the whole is imbedded. The tips of the linin filaments project slightly beyond the pellicle as nerves.
- B. Diagram illustrating the division of the unit; the linin threads in or near the plane of division split longitudinally, while those in or near the plane joining the centres of the daughter units simply lengthen out.
- C. An optical section of the three-dimensional network which would result from repeated incomplete divisions of such a chromidial unit; the chromatin masses divide completely, but the linin threads, though they lengthen and split, are never ruptured.

mentally grasping what we call our "first unit," we find it to be a "chromidial" unit, with the following constitution. Its centre of activity is a minute mass which takes stain and is consequently called chroma-

tin; from this mass radiate short filaments, so fine that no microscope can detect them unless, as it were, by accident, *e.g.*, when small quantities of staining material are present on them.¹ These filaments penetrate into the heart of the central mass and, judging from the later phases, ramify through it like a network. Distally, each filament ends in a kind of skin which covers the whole mass. Between the skin and this central mass is some fluid matter which is not an essential part of the whole.

The chromidial unit is thus a stellate, linin-chromatin system, probably embedded in a minute drop of albuminous fluid, to, or slightly beyond, the surface of which the filaments extend. An organism so constituted would absorb nutrient matters from the environment, while excretory matters would be carried outward along the filaments and to some extent, at least, deposited round their tips. These deposits, spreading laterally, would together form a simple pellicular envelope as a protective covering to the whole.

All this, perhaps, sounds very fanciful and so, indeed, it would be without the evidence that can be produced, which is partly direct, partly derived from the other periods. A brief summary of the direct evidence given in Part I, Chapter I, must here suffice; nearly all that follows in the five subsequent chapters is also evidence, though of an indirect kind.

A minute analysis of protoplasmic tissues (including under the term "tissues" the cell itself) in order to discover the essential structural elements of protoplasm, shows two factors to be constant and invariable: (1) minute masses of chromatin which may be called by

¹ See Pt. I, p. 34 on the conditions of the visibility of the filaments.

the familiar name "chromidia,"¹ individually so small as to be visible only under the very highest powers of the microscope, but visible enough when aggregated into larger masses as chromatin, and (2) a filamentous network, the fibrils of which are of such extreme tenuity as also to be visible only under the very strongest lenses, or when aggregated into strands and specialised into some of the well-known fibrous tissues. The positions and courses of single fibrils can, however, at times, be traced by the presence upon them of rows or streams of chromidia, or of other minute coloured bodies.

The ordinary association of the chromidia and the filaments, when building up protoplasmic masses of any size above the most minute, takes the form of a network, the chromidia being arranged as nodes of a "chromidial net." All the more developed and specialised appearances of protoplasm, even in the most complicated and highly differentiated tissues, are explicable as complications of this network; clumps of chromidia form chromatin bodies, while different arrangements of filaments give rise to fibres of all kinds. Further, hard or elastic matters may be regarded as due to chromidia having combined with other substances to form organic concretions which are then deposited upon the filaments to form skeleton; or, again, meshes of the net may expand and give rise to great vacuoles or an alveolar structure. There is not a single known protoplasmic structure that cannot be deduced from this simple network arrangement and these two essential

¹ The chromidium is not a known quantity in the strictest sense of the word. What are called indiscriminately chromidia are minute deeply staining bodies, masses of chromatin, which, under favourable circumstances, can be seen with a very strong microscopic lens in association with an extremely delicate non-staining network in protoplasmic bodies.

structural elements of living matter. Chromidial nets, as elementary protoplasmic structures, are coming more frequently and steadily into view as microscopic lenses are perfected. It is not without significance to note, in passing, that the primitive network itself seems to be most frequently seen under the microscope when active physiological processes are taking place within the protoplasm, processes which involve small areas of reconstruction.

A network, however, even the simplest, could not have been the primitive arrangement of these two elementary factors of protoplasm. There must have been some simpler combination of chromidia and filaments.

One such combination is suggested by regarding this net as the result of colony-formation; any such network may be considered as a multitude of chromidial units joined by the extremities of their radial filaments (Fig. 43, C).

That such a unit might, by colony-formation, have led on to the cell, just as the cell led on to the Metazoa, is, of course, no new idea. The granular theory of Altmann embodies the same conception.¹ The granules are small masses of chromatin, like the chromidia, but Altmann's theory made no mention of any filamentous elements such as I have claimed for the chromidial unit, and hence he had no means of explaining how his granules could build up colonies.² Indeed, the non-recognition of the filaments as a persistent element in protoplasm appears to me to have been one of the

¹ *Die Elementarorganismen und ihre Beziehungen zu den Zellen*, Leipzig, 1894.

² See further, Chap. XIX, on the same difficulty with regard to the cell.

chief causes of the temporary stagnation which has fallen upon cytology as a progressive science. It was certainly one of the reasons of the non-acceptance of Altmann's theory of the building up of the cell by a colony of granules.

As to the existence of the filaments even in the minutest organism there can be no doubt now we know that such a minute form as *Bacteria Termo* has flagella, while the latest figures of micro-organisms show them as consisting practically of small chromidial networks, not unlike our hypothetical unit, only, instead of having one chromatin granule at the centre, there are numerous masses suspended upon the network.

Starting with the organism we have described—the "chromidial unit,"—let us follow its development.

By the absorption of nutrient matters from the medium, the organism grows, *i.e.*, merely enlarges in size, without necessarily undergoing any change of shape or, so far as we know, of internal constitution. At a certain stage of growth, apparently when it has reached some maximum size, the startling but well-known process of dividing into two takes place. Division may be complete, in which case two stellate linin-chromatin systems are produced where there was formerly one, or incomplete, in which case we have two minute chromatin centres joined together by their linin filaments. If these two again incompletely divide, it is obvious that we have the beginnings of a three-dimensional linin network with chromidia at the nodes (see Fig. 43, C).

The way in which the chromidia, and, with them, the filaments, divide so as together to form a continuous

system, is illustrated in Fig. 43, B. All the filaments in or near the plane of division split longitudinally; all those in or near the line joining the halves simply lengthen.

This division of the chromidial unit, with halving of the chromatin mass and splitting of some of the filaments and lengthening of others is obviously an extremely complex process. It means a very remarkable molecular and histolytical rearrangement resulting from some extraordinary energy of segregation. To this energy of segregation I would call special attention; it will be mentioned again and again in the sequel, acquiring each time a profounder significance.

By continuous multiplication always (and apparently only) brought about by this remarkable process of doubling division of the chromidial unit, homogeneous chromidial networks of almost any size may be produced. Large or small, these masses are always, in essence, organic though undifferentiated wholes. They are not mere swarms of separate units, which was the insuperable obstacle in Altmann's theory, but units threaded together by continuous networks of linen threads; the minute chromatin granules may be regarded as centres of chemical activity, while the threads are nervous and contractile. Such colonies of chromidial units are, so far as we can reconstruct them, the most elementary masses of homogeneous protoplasm known to us.

Launched on to the planetary surface, such homogeneous masses must inevitably lapse into heterogeneity. I say inevitably, because it is hardly possible that large organisms with so elementary a constitution could long remain undifferentiated. It is, therefore, of some significance to find this simple constitution persisting

to-day only in very small organisms¹ and, occasionally, as stated above, showing itself in minute specialised areas of cells at times when transformations of some kind are taking place. Even if, by chance, organisms of any large size ever did exist with such a simple and delicate structure, it is not likely that their remains could have been preserved in any of the sedimentary rocks. There is, of course, the possibility that certain of them may have had skeletal deposits in the shape of spicules or small nodules built up upon the filaments of the network, but, in order to leave any discoverable marks among the coarser materials of the earth's crust, such spicules would have to be larger or tougher than any that could be attributed to so delicate an organism, or they would have to show some arrangement definite enough to catch the eye.

The fact that the cell admits, as we shall see later, of being regarded as a special condensation of a network of the chromidial unit, seems to point to the existence of such large homogeneous networks. Any chromidial network that could be differentiated into a cell must obviously have included many hundreds, nay thousands, of chromidia. But this is somewhat anticipating; the strength of this argument will be better appreciated when the remaining periods have been described. In the meantime, since such complicated organisms as the cell, deducible from a chromidial network, exist, it will be assumed that chromidial networks existed large enough to give rise to them.

In order to understand the lines of differentiation which the delicate organisms of this period would follow,

¹ See Schewiakoff's figures reproduced in Pt. I, Fig. 1. The bearing of Bütschli's theory of protoplasmic structure on the view here adopted is discussed Pt. I, pp. 18-20.

we have to ascertain what their essential living activities would be. The first of all functions for the maintenance of life is to obtain nourishment for growth or for repair of waste. The chromidial unit, and consequently all its immediate derivatives, obtained such nutriment by direct, *i.e.*, chemical absorption of matter from the medium. There may have been nourishing matters free in the immediate environment and obtainable without effort, but other food materials, and these would be the most numerous, could only be obtained by the action of secretions chemically disintegrating the contact-surfaces of external bodies. With growth in size, the more central chromidia would find themselves further and further from their field of action, the absorbing surface of the organism. For this and other reasons, we might expect (1) that the chromidia would tend to migrate towards the surface; (2) that they would tend to form groups for the concentration and localisation of their chemical activities; (3) that this grouping of the chromidia would lead to some rearrangements of the linin threads on which they are suspended: and (4) that these rearrangements of the filaments would become specially pronounced as soon as rudimentary powers of movement and, later, even of locomotion, required some of them to be differentiated for contractility.

Here, then, we have two preliminary steps in differentiation which are of special interest because we shall find them repeated in each subsequent period as exactly as the increasingly complex conditions will allow; clusterings of the chromidia into organs of chemical activity, and rearrangements of the filaments for nervous, muscular, or synthetic functions. I propose to designate the former rudimentary "organ-

formation," the latter rudimentary "tissue-formation," although the distinction is not, of course, very rigid. Such clusterings of organs and groupings of filaments would take place in as many different ways as there were different environmental stimuli to which the chromidial networks were exposed, and to which, at such an extremely simple stage of complexity, they were capable of responding.

With these principles of differentiation acting upon such formative material, we can sketch, in general outline at least, the forms that would be assumed. In the first place, considering the fundamental characteristics of protoplasm, we are justified in dividing them into stationary and free-living forms, the former being those which settled on some nutritious surface and obtained, by the exercise of their chemical organs, an abundance of food while letting their contractile and nervous faculties die down to a minimum, the latter those which developed these functions.

The differentiation of stationary forms of such an extremely simple protoplasmic constitution, and armed only with minute chemically active organs, would have to be such as to allow these organs to act at or near the surface, so as to be as close as possible to the medium from which nutriment was to be extracted. This almost precludes the possibility of any massive forms having much chance of success. Small, round, oval, or thread-like bodies, which could be actually immersed in the medium so as to have the whole surface available for absorption, would thrive best. The internal organs in these would be close to the surface. The myriad "germs of life," the Microbes and other primitive forms, comparatively recently discovered and still the object of diligent research, may be regarded as varia-

tions of the chromidial unit or of small specialised colonies of chromidial units. Very large systems of fine branching filaments might, however, be developed where the nutrient matter was dispersed through a penetrable surface.

Among the free-living forms I do not include those whose habits of life are in reality stationary, locomotory cilia and flagella being possessed merely for occasional purposes. By free-living forms I mean only those in which active locomotion is a necessary part of the regular life-habits. First of all may be mentioned the ciliated or flagellate forms with scattered chromatin. They exist in vast numbers, but are usually classed with the cell as Protozoa. They differ from true cells only in that their chromatin is still more or less scattered, whereas in true cells, the chromatin is gathered into a central nucleus. The organisms referred to show interesting variations as to the distribution of the chromidia; in some, the chromatin is present in small, scattered granules of different sizes, which may be provisionally regarded as different sized clusters of chromidia. In others, similar granules may at one time be very scattered, at another grouped together, such changes of position having been noted even in one and the same organism.¹ These organisms are generally described as having a "scattered nucleus," but there is a decided tendency now to regard them as stages in the evolution of the true nucleated cell, and this, of course, from our point of view, they must be. Indeed, the perfected nucleus, in which the bulk of the chromidia are clustered together in the centre of the organism, is at least one very natural culmination of this line of differentiation.

We could certainly have no more cogent witnesses

¹ See Pt. I, Chap. III. p. 30 and Figs. 8-13.

for our period than these elementary Protozoa. They lead up in the most natural manner to the cell and, on account of their active predatory habits, seem to deserve the name given to them. They are pre-cellular Protozoa and the cell is, as we say, their natural culmination. The climax is reached when all the chromidia and chromidial clusters find themselves, at least during periods of rest, in a central position in the organism, massed upon the filaments of a special tangle of the network, from which central tangle all the rest of the network radiates outward toward the surface.

The cell having come into view, we might advance to the next period. But we must linger for a moment over some of the lessons of the chromidial period. It is clear that the morphological transformations of the chromidial network into the cell are those demanded by the physiological needs of the organism interacting with its environment. It is this interplay which calls out the functional activities of the organism. This is its life, and life is at no time intelligible without a comprehension of its physiology. In this period, the physiological evolution outweighs in importance the morphological changes. Indeed, so fundamental were the functions acquired during this period by the different chromidial clusters, that they have been for the most part retained as still essential to life. I do not deny the possibility of some having died out and of others having been secondarily acquired. But, from this time, evolution has been mainly occupied in building up organisms as so many different mechanical frameworks specially designed for the better co-ordination and application of the elementary chemical functions acquired during the chromidial period. We may, therefore, assume that the chief chemical activities of

later and larger organisms are due to the more efficient application of powers now learned. Modifications and differentiations would naturally take place as, with increasing complexity, better arrangements for their utilisation and concentration developed.

To this time, therefore, we may refer the origin of some, at least, of those specially active bodies called ferments, which attack and chemically dissolve foreign substances but repair their own waste as fast as they wear away, thus exhibiting one of the essential phenomena of living substance. Ferments have to be regarded, I believe, as living organisms. Indeed, the suggestion naturally arises that they may be free units persisting from some period still earlier than that of the chromidial unit, just as, in larger organisms, free cell-units (blood corpuscles, leucocytes, etc.) are known to survive and to play an important part.

Such, then, is our first period, which arises by the colony-formation of a minute organism that we had to reconstruct. The chief notes of the period are just what we should expect, since life was at this time still, as it were, emerging from the inorganic and becoming organic, a change which seems to have been brought about by the gradual development of complicated systems of linen threads with nervous, muscular, and synthetic functions. We may say that, in this period, organic life begins in earnest to invade and storm the environment, no longer merely as a chemical equilibrating with its planetary medium, but as a nervous and muscular machine, learning to respond to or equilibrate with as many of the planetary conditions as it can cope with and survive. Every subsequent period will involve an account of the same process or series of processes, which are of the very essence of life, though, at each

step, we shall find ourselves upon a higher level, dealing with organisms which are becoming more complicated and thus able to cope with larger and more complicated environments.

CHAPTER XIX

THE SECOND EVOLUTIONARY PERIOD, THAT OF THE CELL UNIT

A FIRST glance at the Cell unit (see Fig. 44) reveals a somewhat startling resemblance to the chromidial unit, the difference between them being chiefly one of size. In both units the chromatin is massed at the centre and, from it, linin threads radiate outward. This is no accidental resemblance, as we shall find when dealing with the units of subsequent periods; all the units alike are characterised by the fact that their physiological and morphological centres as nearly as possible coincide.

When the cell is regarded as the second unit of structure in a series and as having consequently been built up by the first unit, the nucleus, its chief organ, has to receive a new interpretation. It is the natural culmination of the process of clustering of the chromidia or central organs of the chromidial unit. In the typical cell, all the chromidia have, in fact, collected into the centre, a change which involves a complete rearrangement of the filamentous network. All the chemical forces become grouped in the centre, equidistant from the surface, and a radiating network of linin filaments brings centre and surface in nervous communication. Such an organisation is complex enough for almost any specialisation.

The chromatin, in the cell, appears to be enclosed in a vesicle with a membranous wall, but our deduction of the cell by gradual differentiation of a continuous network compels us to regard this membrane as a felting or matting of the outermost filaments of the central tangle,

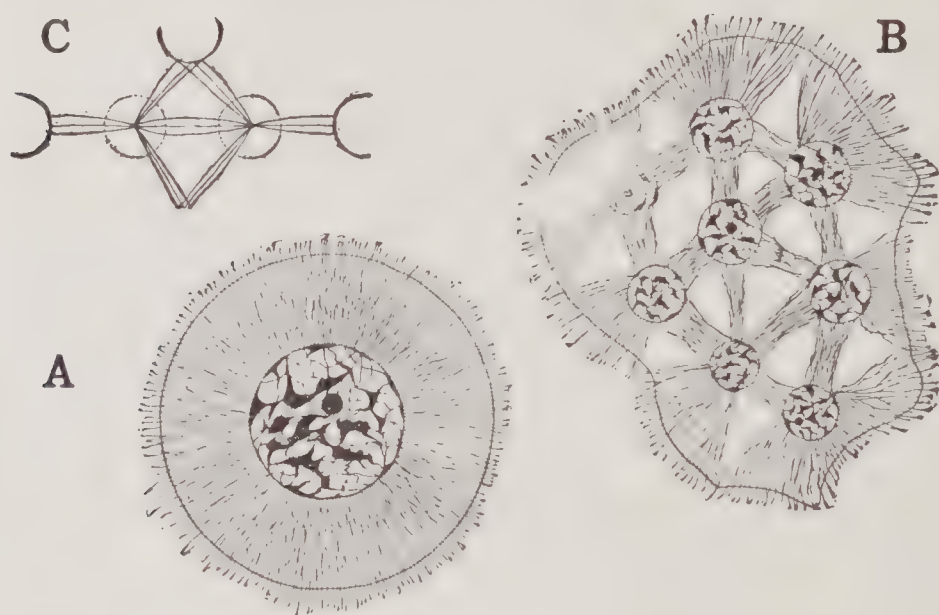


FIG. 44

- A. Diagram of the Cell Unit, showing the chromidia clotted together in masses upon a special central tangle of the linin network; this forms the nucleus or chief organ of the cell, and may be regarded as built up by the union of all the chromidia of the chromidial network. From the surface of the nucleus, the rest of the filamentous system radiates outward, ending in a fringe, frequently of vibratile cilia.
- B. Optical section of homogeneous aggregate built up by the cell.
- C. Diagram illustrative of the process of cell division.

and consequently to consider the intranuclear network as being in direct filamentous continuity through this felt-like membrane with the radial system stretching from the nucleus to the outer surface of the whole organism (Fig. 44, A).¹

It will be seen that we are here ascribing a very

¹ See Pt. I, pp. 45-47.

definite structure to the nucleus; it is not only a cluster of chromatin granules variously arranged in the centre of the cell, but it is a special tangle of linin threads sharply separated by a distinct feltwork membrane from a much more simply and uniformly arranged radial network at the middle of which it lies. The chromatin has hitherto been generally regarded as the one important element of the nucleus, but this view entirely overlooks the morphological and physiological importance of the linin system. In my view, both chromatin and linin filaments are essential structural elements of protoplasm.

This, very briefly stated, is the organisation of our second unit, the cell, the most important of whose elementary life processes, its method of feeding, first claims our attention.

The chromidial unit, we saw, obtained nourishment solely by chemical absorption. The cell was large enough to add another method of feeding. Besides being able to extract all it needs directly by chemical action from the medium, including the air, and retaining and specialising for that purpose the chlorophyll organs, it could also assimilate nourishment ready made in particles of organic matter which it incorporated and dissolved internally. This latter specialisation it was that started animal life, with its particular development of linin filaments into muscles and nerves. A cell, to feed by the original method, required only chemical activity, whereas the obtaining of nourishment by the later method involved the development of locomotion. The original method consequently led to vegetable, the latter to animal life. Animal and vegetable life are alike, of course, in the fact that the organism, in each case, extracts the necessities of life

from the environment. But they are not rivals, for they tap different supplies. The one succeeds by organic quiescence, the other by constant and ever-changing intercourse with the environment. In the plants, the original network remains unspecialised so far as its elementary nervous and contractile functions are concerned, but it is very highly specialised for synthesis, *i.e.*, for the building up of "cell-walls," for the formation of woods, barks, and covering membranes, not to mention the perpetual transportation of materials from place to place, often over great distances.

Confining our attention to the animal kingdom, we find that particles of organic matter were at first engulfed by cells at any point of the surface with which they came into contact, the residue being ejected at any point. This was the primitive condition. But gradually, in the interest of larger size, more rapid motion, and stronger cilia, a thicker external layer was developed,¹ and that necessitated the localisation of an entrance through which food particles were conveyed inwards to the soft internal protoplasm. The position of the opening would tend to be such that the motion of the cilia would cause a current in the water to bring the nutritive particles into it as into a simple kind of gullet. Here are possibilities of great range of variations in small structural details, all of which would depend upon the special method of feeding, which would also vary according to the character of the food supply most available. There still exist, as we should expect, an enormous number of small, unicellular or uninuclear organisms possessing essentially these characters and

¹ On the formation of pellicles as an active, vital principle see Part I, Chap. III., pp. 71-76.

yet varying in fine details of arrangement. Indeed, a far greater range of variation is recognisable among the cells than among the much smaller Microbes, so far as the latter are known under the microscope. This fact is obviously to be correlated with the wider range of environmental conditions to which the larger cell is exposed, as compared with the smaller Microbe. The latter was characterised by the simple, direct absorption of matter, the cell is distinguished, *physiologically*, by the far greater number of sensitive points presented by the radiating filaments and also by greater muscular strength for rapid locomotion and for the ingestion of solid, organic matters which can then be broken down and absorbed within the organism. *Morphologically*, it is distinguished by structural modifications for the attainment of this end. In order, however, to reach still higher levels, the cell has to increase greatly in size and to have a still greater number of sensitive points radiating in all directions, changes which can come about only by colony-formation.

At a certain stage of growth, the individual cell, like the chromidial unit, divides into two halves. The process of division is more visibly complicated in the cell than in the chromidial unit. We cannot obtain any insight into the minute molecular histolysis of the latter, nor even see that any such takes place, but the puzzle presented by the necessary rearrangements of the chromatin masses and of the network is visible in the cell; the splitting of the equatorial filaments and the lengthening of the axial, which we had to assume for the chromidial period, can actually be seen taking place (see Fig. 44, C).

The division of the cell, like that of the chromidial

unit, may be complete or incomplete. In the latter case, the result of repeated doubling division is to build up colonies large and small which are, from the first, organic wholes, as were the chromidial networks resulting from the multiplication of the chromidial unit, only now we have the nuclei instead of the chromidia at the nodes and, instead of single linin filaments from node to node, we have strands of anastomosing filaments running from nucleus to nucleus. In this way, homogeneous cell-aggregates were built up which, in optical section, had essentially the structure shown in Fig. 44, B. Here we have the explanation of the secondary co-ordination of the cell units, that stumbling-block of the prevailing cell doctrine. We need no longer wonder how a heap of cells which appear, under the microscope, as distinct from one another as a pile of billiard balls, can possibly grow together and become one single organism, nor need we ask why some cells agree to put out processes through the heap to supply a future nervous system and others stretch out and attach themselves here and there to start a nervous system.¹ For they do none of these things. The chromidial and cell aggregates produced by incomplete division have never been anything but *organic wholes*. Their continuous linin-chromatin frameworks have been gradually differentiated into nervous and contractile systems of every degree of complexity according to the demands put upon the organism. Those observers who have seen nerve processes "growing out of embryonic cells" have, in reality, seen protoplasmic materials travelling out along invisible linin filaments² which

¹ Cf. on neurone theory, Part I, pp. 222-235.

² Cf. reference to the "spinning activities" of the blastomeres of the dividing eggs, Part I, p. 93; see also on the cell-bridges of *Volvox*, p. 106.

are to be specialised into the primitive fibrils of the definitive nerve fibre. Indeed, any organ that is produced in any undifferentiated cell mass is but a modification of some existing structural complex. Let us take the skeletal supports as an illustration. The deposits of waste matters upon the filaments—deposits of the kind and strength required—build up skeletal supports to counteract the muscle pulls or to act as protective coverings, exactly where they are needed for the efficiency of the complex. I repeat that all structural developments are but modifications of different parts of a continuum, and examples of the “gravitating” of homogeneous masses.

It is comparatively easy to sketch the rest of this cell period, for it follows the lines laid down in the chromidial period very closely. Just as the chromidia of the chromidial networks began to cluster together for the formation of simple tissues and organs in which the various activities of the chromatin might be concentrated and differentiated, the filaments becoming rearranged for elementary neuro-muscular functions, so here the nuclei cluster for the formation of organs, digestive, secretive, and excretive, and the connecting filaments, owing to this very clustering of the nuclei, are collected into strands to be variously specialised. In this case, the larger size of the organisms, and the more active habits demanded for the capturing and ingestion of solid particles, put much severer strains upon the filamentous portions of the framework and lead to their special development and to a greater range of differentiation. The linin filaments which, owing to their original extreme tenuity, could hardly be seen and thus failed to be recognised as permanent or essential protoplasmic structures, now that they are grouped

into strands, with protoplasmic and other coatings, gradually become the conspicuous fibrous tissues of anatomists, far more conspicuous, in fact, than even the cells themselves. Some of these strands became coated with elastic and skeletal matters for support, some specialised their primitive contractile, others their nervous functions, so that neuro-muscular and skeletal systems arose *in situ* and, however ultimately specialised, functioned as connected systems from the first, connected with one another and with the rest of the body as integral parts of the whole.

Any one who has the slightest acquaintance with the problem of the nervous system and the theories that have been put forward to solve it¹ will, I think, gladly welcome this simple and workable solution. The earlier zoologists, indeed, long ago postulated some primitive continuous network out of which the different nervous systems might have been developed. Our linin-chromatin system is what was wanted. As an essential structure of all protoplasm, it even supplies us with an explanation of the faint nervous phenomena seen in plants, though it is in animals alone that it has been specialised into complicated neuro-muscular systems.

Endless are the possibilities of specialisation afforded by different clusterings of the nuclei and groupings of the strands, of these originally homogeneous cell-aggregates. There was no reason why the nuclei should not group in thousands of different ways, rearranging the filaments in accordance with their requirements. Four examples may be given of the more

¹ Cf. especially the recent neurone theory, based entirely and solely upon the fanciful interpretation of part of the ramifications of metal solutions through tissues, in the light of an erroneous cell doctrine.

important groupings that have survived and are of special interest as stages of increasing complexity.

In the Sponges, which have departed least from the simple cell network, the characteristic "whip-chambers," are produced by the simplest rearrangement of the nuclei, while the very primitive spicular skeletal system has, I believe, been built up by deposits upon specialised portions of the fundamental network.¹

In the Echinoderms, the skeleton is almost equally primitive, but localised into subdermal plates and arranged so as to be only slightly less hampering to further development than is the arrangement in the Sponges.

In the Molluscs, the skeleton takes the form of a dorsal protective shield or shell.

In the earlier Coelenterates, there was originally no hard skeleton and, as long as the skeletal condition was retained, these forms remained almost as plastic as the cell.²

These are all very natural specialisations of cell networks, but others of considerable size with fewer nuclei would result from small colonies, and it is some support to our view to find known forms obviously deduced from much smaller colonies, even down to the smallest multiple of nuclei, both animal and vegetable. Among the former we may mention the Dicyemidæ and even the Infusoria with more than one nucleus, such as *Paramecium*. Among the plants we may recall *Volvox* and other small algæ.

One other early cell-colony deserves attention. The Myxomycetes are cell networks without any vigorous development of the fundamental filaments to hold them together. They sprawl over the ground,

¹ Part I, p. 101.

² See Part I, pp. 121.

or rather over the surface of dead organic life, and resort to the original method of extracting nourishment by chemical dissolution and absorption by surface contact. Opinions have differed as to whether they belong to the animal or to the vegetable kingdom; they remain somewhere on the borderland. I am inclined to place them here among the animal cell-colonies because of the absence of chlorophyll and of the typical cell-walls of plants, although I admit that these may have been secondarily lost.

All distinctively animal cell-colonies, however, followed the habits of their cell units in actively taking in solid particles of food, and it can be shown in detail that their definite morphologies, as Sponges, Echinoderms, Molluscs, or Cœlenterates, turned upon the different methods adopted for this purpose.

The ingestion of solid particles necessitates a large amount of differentiation, in the first place for the mechanical process of catching food and of transporting it from without into the interior. Then cavities, or one cavity, for its reception had to develop, with special arrangements whereby the chemical activities of the chromidia and ferments can dissolve it, so that the whole organism can absorb it, the diffusion being perhaps aided by special channels. Lastly, a mechanism was needed for the discharge of indigestible residues, with another set of channels for the carrying away of waste. The elucidation, in the light of the protomitomic system, of the different ways these changes and functions have been effectively carried out must be left to comparative morphologists and physiologists.

The one point in the morphological transformation

of the cell-colonies that I wish here to emphasise is the natural formation of cavities and channels of all sorts, whether as receptacles for ingested food or for excretion. In the chromidial networks, the simple expansion of the meshes sufficed and such expansion also took place in the cell network, though the fact has been quite obscured by the teachings of the old cell doctrine. Any expansion of the meshes of the cell network would lead to a pushing outward of cells; we consequently find all the surfaces of the Metazoa, external or internal, lined by epithelia. According to the prevailing view there was one original epithelium, and all later epithelia have to be deduced from this primitive early layer which formed the wall of the blastula, either by processes of invagination or delamination. There is, of course, truth in the general fact that epithelia are, as a rule, deduced from pre-existing epithelia; processes of invagination are common ontological phenomena. But there is no need to limit the primitive epithelia so rigidly to one, for, in the differentiation of the homogeneous cell networks, nuclei as centres of chemical energy would naturally migrate to the surface so as to be in contact with the external medium.¹ Such migration would be specially active towards a cavity in which food stuffs were present to attract them. This would account for the strong individuality both of the "hypoderm" and of the "ectoderm" as the two oldest animal tissues.

Another point worth noting is that the appearance of a cavity within the network would of itself necessitate a

¹ The migration of nuclei can be easily traced by any comparative study of vertebrate retinas, young with old, and the migration can be shown to be towards regions of greatest physiological activity.

felting of the filaments pushed on one side. All the tangentially arranged filaments would be matted into a neuro-muscular basement membrane,¹ from which the chemically active nuclei would project radially inward into the cavity. The movement of the nuclei towards the cavity would also lead to a radial arrangement of filaments round it to subserve the synthetic functions of the particular epithelium for bringing excretory matter to be discharged into the cavity or for carrying away the products of digestion. This example of the original production of epithelia must here suffice. As structural elements in the building up of the organs of the higher forms they are as characteristic as was the clustering of the chromidia in the earlier period.

Along these lines of differentiation the homogeneous cell-colonies lapse into heterogeneity.

We can now sum up those points that are essential to our main theme, *i.e.*, those that show how closely this period has repeated the chromidial period.

1. The units of the two periods resemble one another in their essential architecture, differing chiefly in the much greater complexity of the nuclear chromatin centre and of the radiating network of the cell.

2. Both units multiply by division.

3. Both, dividing incompletely, form homogeneous aggregates which are three-dimensional networks, with the centres of chemical activity at the nodes.

4. Each gives rise to aggregates which vary greatly in size. Chromidial aggregates of small size, *e. g.*, the

¹ This may be so thin as to be a mere basement membrane, which, being structurally a feltwork of linin filaments, may be very elastic. The subject of the fine structure of epithelia is dealt with at some length, Part I, Chap. IX.

Microbes (see p. 336), are paralleled by small cell-aggregates, say, for instance, such forms as *Trichoplax*, whose position has hitherto seemed enigmatical.

5. Both become differentiated in essentially the same way, the unit organs clustering together to form the colonial organ. In the chromidial aggregates, the chromidia form the nucleus, in the cell aggregates, the nuclei form the digestive cavity of the Metazoa, while (anticipating somewhat) the matting of the filaments of the chromidial units to form the nuclear "membrane" very closely resembles the matting of the strands joining the nuclei which line the food cavity into the neuro-muscular layer which yields the digestive epithelium of the *gastræa*. Both nucleus and digestive cavity are essentially contractile vesicles.

6. In both units, again, the resulting organisms are due to the different kinds of response demanded of them by the external forces, attractive and repellent, of the environments in which they settle.

7. Some of these resulting organisms settled down to stationary lives, others became active and free-swimming. It was one of these latter, the free-swimming *Gastræa*, and, be it noted, the one which most nearly resembled the cell and the chromidial unit in structure and manner of life, which, as we shall see, became the next unit.

Now it is quite impossible that a parallelism such as this should be pure accident. It is so extraordinary that it must help to establish the view that our series of units is rhythmical. Though none of the later periods resemble one another so closely as the two we have just compared, the resemblance is kept up as nearly as possible under the altered conditions of increasing complexity. So true is this that, in cases where we seem

to have lost our way among the multitudinous and bewildering facts of text-book zoology, we can find it again by keeping close to the formula established by the details of these two periods.

CHAPTER XX

THE THIRD EVOLUTIONARY PERIOD: THAT OF THE GASTRÆAL UNIT

THE unit of the period following that of the cell, which we may call the Cœlenterate period, is the polyp or Gastræa.

There were at least two forms of the gastræal unit: one which built up the Alcyonaria, the other the true gastræa.¹

The great importance of the gastræa was long ago recognised by Professor Haeckel,² although the part it played in the evolutionary process could not possibly be realised until colony-formation was accepted as an important factor in evolution. Further, the gastræal or cœlenterate period has long been regarded by zoologists as a distinct period in which the bulk of the organisms produced are colonies of polyps. So clear, indeed, is this point, that the cœlenterate period, minus the Alcyonaria, could be taken bodily out of modern systematic zoology and find its place in our rhythmical series.

The gastræal unit arises directly from a cell-network by the formation of a large nutritive cavity, all the nuclei, during this process, crowding outward to

¹ For the difference between these two units see Pt. I, p. 127. The gastræa we shall here describe is not exactly the orthodox gastræa, this latter being the ideal product of the prevailing cell doctrine.

² See also Part I, p. 123.

form the wall of the sac thus produced.¹ In this way, the gastræa gradually comes to resemble the two units that preceded it.

The chromidial unit, it will be remembered, had the chromatin, which represented the store of its chemical forces, massed in the centre and, from this mass, the linin filaments radiated outward. These filaments, besides being contractile and having synthetic functions, were also essentially nervous. The chromidial unit might be described as an organism bristling, as it were, with exposed nerves. The cell has essentially the same character. All the active chemical forces represented by the chromatin are again massed at the centre in what is called the nucleus, and from this, again, the linin filamentous network radiates outward. It is along these rays that the energy stored in the nucleus is expended. Waste matters are sent along the linin filaments to the surface; the filaments themselves contract or lengthen, their tips are caused to vibrate and, in this last case, chromatin can be traced on its way from the nucleus for the maintenance of the energy expended.² Lastly, all or, at least, a large proportion of the filaments carry nerve stimuli as perhaps their most fundamental function, a function which becomes specialised in some filaments, interfered with in others, and may even be kept entirely in abeyance by their having to do other work, such as contracting and expanding as muscles, building up skeletons, or even forming lines of drainage.³

¹ So far the old theory of invagination is endorsed, but the term invagination is far too formal for the simple fact.

² See Part I, Figs. 14 and 16.

³ I am of course aware that this simile is far too coarse for the extremely delicate molecular changes which lie at the base of the vital processes. It is used more with reference to the results obtained than to the methods of obtaining them.

The cell, being much larger than the chromidial unit, comes into contact with a larger environment; and, further, it is vastly more complex and its reactions to its more extensive environment are more intricate and powerful.

It is impossible to suppress surprise at finding that

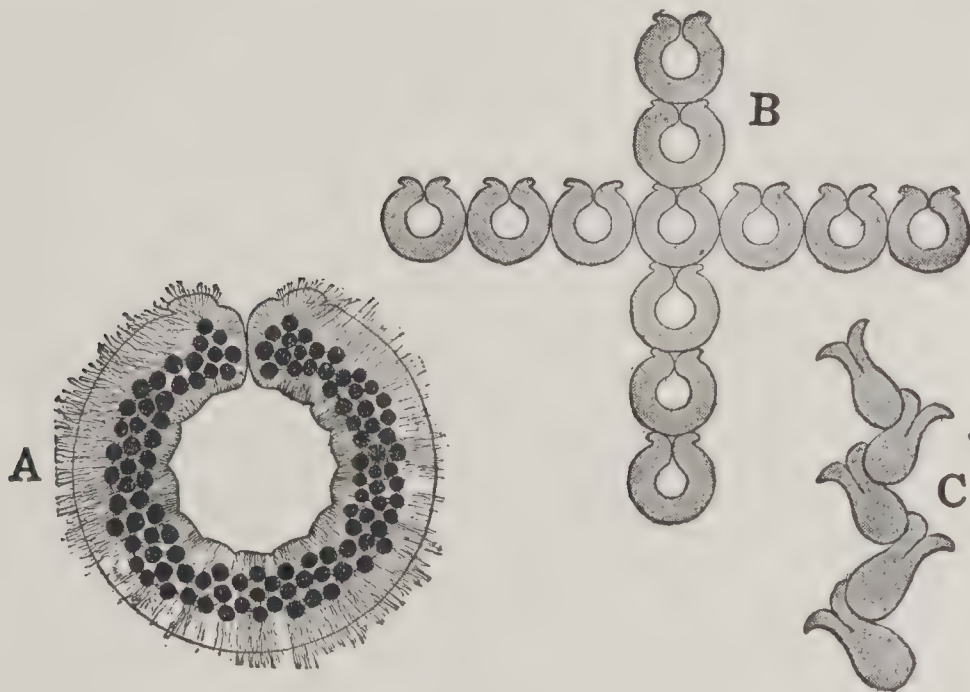


FIG. 45

- A. Diagram of the Gastræal Unit, in which a central digestive cavity has arisen in the original network.
 B and C. Some of the forms of colonies the gastræal unit can produce. The vertical row, common in the early corals, involved the death of all but the latest added unit at the top. The posterior budding that takes place in the Annelids is illustrated in C.

the gastræal unit, in spite of being built up probably of many thousands of nuclei, repeats the essential form of both the cell and the chromidial unit. All its chemical forces are once more stored in the centre, matted together round a large central cavity. In place of the nucleus, as a turgid vesicle filled with chromatin masses, and some highly refractive fluid called the nucleoplasm, we have a digestive cavity of great size, walled round

by all the displaced nuclei (Fig. 45, A). Into this, food masses are brought from without through a mouth, and in it are dissolved by the chemicals discharged from the nuclei lining the inner surface of the wall of the cavity, which is called the digestive epithelium. The juices resulting from the action of the chemicals upon the food are then absorbed by the organism as a whole.

The food within the digestive cavity of the gastræa is no part of the organism, and would be disregarded but for a suggestion that arises automatically from the resemblances above detailed. The whole digestive apparatus is essentially a store of energy, as is the nucleus. But, in the gastræa, it is also a producer of energy. May we not conclude that the nucleus is also the same? Following up this idea, I would suggest that the juices prepared from the food within the digestive cavity may be the homologue of the nucleoplasm and that, therefore, that refractive and enigmatical fluid might be regarded as a product of the digestion of food particles taken in from without. These would be dissolved and digested in the cytoplasm and the product stored in the nucleus. The nucleoplasm would consequently be the material out of which both the chromatin and the linin filaments are able to grow and repair waste, and without which they could not long perform any of their vital functions.

Further, the massing of the nuclei with the matting of their filaments round the digestive cavity remind one, as already stated, very closely of the felted "membrane," always dotted over with chromidia, round the nucleus of the cell. This comparison is also based upon the resemblances above detailed; both, in their origin, are feltworks, both arise naturally round a cavity or opening, or a specialised tangle appearing in a network. In

the nuclear membrane, the linin filaments remain undifferentiated, as they simply run from chromidium to chromidium, but, in the case of the digestive cavity, they have been specialised; some became coated with elastic skeletal matter to form a tough gelatinous supporting membrane called, in this case, the mesoglæa; others functioned as nerves and others as muscles. With regard to the mesoglæa, we note that elastic basement membranes are not uncommon but, in this case, the membrane functions as a kind of plastic skeleton for the whole organism, such strengthening being very necessary in view of the strains which might be put upon the cavity. All these three, the mesoglæa, the muscles, and the nerves, would form a highly differentiated neuro-muscular and skeletal system for the contraction and expansion, not only of the digestive cavity, but of the whole organism.

From this felting of the cell-network round the digestive cavity of the gastræa, the rest of the filaments would radiate, as in the cell, to the surface (see Fig. 45, A). As in the cell, also, some of the filaments would protrude as cilia, others would convey waste matters to the surface, while the marvellous stinging darts, which are normally thickly studded over the exposed parts of gastrææ, may be regarded as derived from filaments carrying away waste matter which have become coiled up like spiral springs and, loaded with poisonous matters, dart out with force enough to penetrate any soft protoplasmic bodies with which the organism comes into contact.¹ This strange specialisation of the radiating filaments which is common, I believe, to all Cœlenterates, is found in one large group of sedentary forms, the madreporarian Corals, in the

¹ See Part I, pp. 43 and 127.

shape of darts over the upper free half of the flexible body, while the waste matters, carried outward from the lower parts, are hardened with lime salts and deposited upon an external fringe of the filaments, like long cilia, so as to form a compact solid skeletal layer built up of spicules.¹

The specialisations of filaments carrying away waste which coats them with hard matter as individual spicules for the building up of a compact outer covering, would necessarily withdraw many of the filaments from being able to function as nerves. It is always possible, however, that the tips of the filaments which coat themselves with skeletal matter may nevertheless come to the surface, or even protrude, and thereby retain some sensitiveness to external physical or chemical stimuli. Still, only those organisms in which the greatest number of surface nerves retain their sensitiveness to the environment, *i.e.*, only those least hampered by surface specialisations, are destined to advance life. The Corals, with their skeletons, are left behind,² while the gastræa, the primitive polyp, with no other skeleton than the elastic membrane strengthening the wall of its digestive cavity, and with its outer wall sensitive to every impact, is able to carry on evolutionary life. Like the chromidial unit and the cell, it is an organism with its centre of force kept in close touch with the environment by a fringe of exposed nerves.

This, then, is the true gastræal unit. The contrast between it and the closely related alcyonarian unit,

¹ This origin of the coral skeleton is more fully discussed in Part I pp. 121-123. The hardening of waste matters upon long, external filaments which, if projecting singly, stand out as radial spikes, is common also in simpler forms (*e.g.* Radiolaria, Sponges).

² See p. 121.

referred to at the opening of this chapter, is instructive. The latter had a smaller digestive cavity and consequently a thicker wall with looser peripheral arrangement of nuclei. There was thus no specially compact neuro-muscular layer. Within this thicker wall, skeletal matter might collect on the filaments between the digestive cavity and the outer surface, there being no need for projection beyond that surface. Such an internal skeletal system would hamper the development of a neuro-muscular sheath.

The difference between the respective efficiency of the two units is obvious. The true gastræa, with its more capacious digestive cavity, not only has larger supplies of energy but, by its powerful neuro-muscular sheath, retains greater freedom of movement for the expenditure of that energy. It is not surprising, therefore, that the products of the alcyonarian unit were outstripped in the race of life by those of the gastræal unit.

The growth of the gastræal unit is necessarily somewhat complicated, for it is no longer a homogeneous cell-network, but one already specialised as to its ultimate shape, and the division of its nuclei has to follow some regular order, so as to attain the definite result required.

It is not, however, the division of the component cells during the growth of this gastræal unit as an individual that most interests us, but the division of the unit itself as a whole, as soon as it is fully grown or adult. Although the division of whole polyps is a well-known phenomenon in the Cœlenterates, I am not aware that it has ever been ranged, as I am here ranging it, in a series with the dividing of the chromidial unit and of the cell, all three being considered as

homologous phenomena. Yet our rhythm shows them to be so. It was difficult enough to imagine the division of the cell, and how great must be the forces necessary to overcome the difficulty of dividing the gastræa, built up of thousands of cells. We should even doubt the possibility of such division if we did not know that it took place. All we can do is to stand amazed at the process and at the energy required to succeed. For it does succeed, and we find the coelenterate period noted chiefly for the variety of colonies produced by the incomplete division of polyps. In face of the difficulties to be overcome in dividing into two equal halves (fission) we are not surprised to find that the rhythm, or rather, the exactitude of the repetition, has to be slightly altered in order to get round and avoid so great an obstacle. What the exact changes in the histolytical processes involved in the alteration are, we cannot even guess, but the result of the change is that the units now begin to divide, not into equal, but into unequal portions, that is, budding tends to take the place of fission.

It is of interest to note that the gradual change from the more difficult equal division to the apparently easier and certainly less paralysing process of budding can be traced in the evolutionary history of the stony Corals. Though these were from the first hampered by their skeletal cups (protothecæ), yet equal division, called in this connection fission, seems to have been the commonest method of multiplication in the paleozoic forms, budding being only an occasional phenomenon. In the Perforata, the most recent of the Madreporaria, fission is, on the contrary, exceptional and budding the rule.¹

Compared with the Madreporidæ, which are recent forms, the

But this alteration in the method of dividing so as to build up homogeneous aggregates is not the only modification necessitated, in this period, by increasing complexity. The one-sided specialisation of the gastræa caused by the development of a localised mouth limits the possible shapes assumed by the colonies built up. Both the chromidial and the cell unit were more perfect units of structure, inasmuch as they were capable of fitting together any way, and of building up homogeneous three-dimensional networks. This is no longer the case with the gastræa. It now has an indispensable one-sided specialisation which has to be taken into account in its attempt to form practical and efficient colonies. It can only form homogeneous masses, or rather groups, in linear or superficial arrangements; a three-dimensional arrangement would inevitably soon destroy all but a portion of the outside layer.

Three of the possible methods of grouping are given in the diagram (Fig. 45, B and C), a linear, a superficial, and a zigzag, the last being due to lateral budding. These will all be recognised by zoologists as having found specialised expression in the ground plans of many coelenterate forms.

Among the animal forms to be deduced from the gastræa we have, first of all, those which are specialisations of the unit itself, and these are both stationary and free-living. Then, secondly, we have the results of colony-formation and these also are either stationary or free-living forms.

Astræids, in which fission is common, are ancient and persistent types. The appearance of double calices in such genera as *Porites* (recent forms normally increasing by gemmation) has puzzled systematists, but may be accounted for by regarding them as sporadic reversions to the earlier method of equal fission which, however, remains incomplete.

Vast numbers of gastrææ became sessile and merely specialised their typical and most efficient organisation. We need only mention the host of sea-anemones as examples of a remarkable increase of digestive surface brought about by means of mesenteries which, in time, draw down the mouth aperture to form a gullet. Some few of these forms developed skeletons of carbonate of lime and became simple Corals, others encased themselves in chitin and formed the single Hydrozoa.

The Jelly-fish are free-living gastræal units variously specialised, often in strange ways. Besides these, there are the Ctenophora, which may be deduced from Jelly-fish that learned to close their bells along one diameter as a secondary and larger mouth, and the Flatworms which can be deduced from gastræal or alcyonarian units browsing with mouth applied to the surface. I suggest, for these, the alcyonarian unit, because of the presence of the large amount of parenchyma which characterises the Flatworms.

But the bulk of the gastræal forms built up colonies—colonies of Corals, colonies of Hydrozoa, even colonies of Flatworms,¹ and the alcyonarian unit also gave rise to colonies.

Where among these, however, are we to look for signs of the new unit? The gastræal period cannot end until such a unit arises. Stationary forms, we know, have no chance in the race upward to raise the level of life and most of the free forms, such as the free-swimming Jelly-fish, the Ctenophora,² and the Siphonophora are highly specialised. The first two of these

¹ *Microstomum lineare* Ehren. and the Tapeworm.

² These can, I believe, be shown to be derived from the ordinary Jelly-fish by the shutting of the bell along one of its diameters, a new mouth being thus produced.

are single gastræal units specialised for habits of life which have not only not advanced but seriously detracted from the efficiency of their neuro-muscular systems. The Siphonophora are, it is true, free swimming colonies, but owing to the uniformity of their environment—the open sea—their specialisations, even when tending to organic centralisation, remain bizarre and completely outside the evolutionary race.

Only a free-swimming colony of polyps in which the units have become so welded together that their neuro-muscular systems have combined to form a much more powerful and efficient system than was possible in the smaller single unit will serve our purpose and for such a form we look in vain among the recognised Coelenterata. In each of the three earlier periods the unit of the next period came to hand without much seeking. But now, at the end of the gastræal period, we find ourselves for the moment casting about and wondering whether there was any other unit at all, or whether, from this time forward, the process of evolution was confined simply to continued lapsing (by the perpetual selection of natural variation) into new environments. Such a process, as we have seen, has no power to raise animals in the scale of life, however highly specialised and complicated they may become. This supposition, therefore, cannot help us and we are driven to assume that some new unit of structure must have been produced by the coelenterate period, but that the gastræal units forming it were so disguised that it has not been recognised as a coelenterate colony. It must be sought for by reviewing the known animal forms higher than those which we have shown to have resulted from the three periods already sketched. Now, none of the segmented animals, which probably outnumber all the rest of the animal kingdom

put together, have yet appeared among the showers of lapsing organisms of the earlier periods. This gives us the clue we require, so that, when we now cast our eyes over the higher forms, we recognise that *some annelidan unit, specialised from a linear series of gastræal units*, could best bridge over the space between the Cœlenterates and the still higher forms.

Linear series of polyps produced by fission are familiar to every student of the paleozoic Madreporaria. They were, however, all fixed and stationary forms, and this must have involved the death and absorption of all the units except the uppermost. We know that no organism had a chance of forming a link in the rising chain of life if it became sedentary and protected itself with a powerful skeleton. Just as both the cell and the gastræa, which became units, were active free-swimming askeletal organisms, which developed their neuro-muscular systems, so it must have been a free-swimming colony of gastrææ which, in its turn, supplied the next, or annelidan unit.

The process may be described hypothetically as follows. We start with a free-swimming gastræa, which advanced energetically and captured food mouth foremost and not like so many of the more specialised free-swimming gastrææ derived secondarily from colonies, which are bell-shaped and swim backwards, opening and shutting the bell alternately. The form we now have to postulate swam forward, by means of its cilia and, avoiding the method of reproduction by fission, budded in that portion of the body where buds would least hinder its efficiency, *i.e.*, at the hinder end. This posterior position of the bud, indeed, would render the organism more efficient as, by adding to its length and also to the number of available cilia, its rapid-

ity of locomotion for the capture of food would be increased.

Gastræal colonies built up in this way,¹ which were both linear and free-swimming, might be expected to appear very early, and such a colony alone, by becoming gradually specialised, could, so far as we can see, produce another unit.

As a matter of fact, these linear free-swimming colonies had a straightforward task in becoming efficient though not very perfect units. An abundant food supply, great activity, and a life-habit which kept all the muscular and nervous powers of the organism on the stretch are assured. This unit is, however, not a perfect unit because, in order to gain speed and activity, it elongates and thus endangers the complete centralisation seen in the chromidial unit, the cell, and the gastræa.

With the unit of the next highest period thus provisionally sketched, we may leave the gastræal period. Except for the two modifications mentioned, the change from complete fission to budding, and the limitation of the possibility of colony-formations to superficial or linear arrangements, three-dimensional networks being no longer practicable to units possessing mouths—it has repeated the course of the cell-period closely enough to permit us to regard it as a link in a true rhythmic series. And we may note how life has been steadily raised from a simple chromidial unit to a powerful organism, tearing about through the open sea, capturing its prey, and undergoing a thousand experiences from its varied environment.

¹ Cf. the short thread-like colonies of *Microstomum lineare* among the Flatworms.

CHAPTER XXI

THE FOURTH EVOLUTIONARY PERIOD: THAT OF THE ANNELIDAN UNIT

OUR first task with regard to this period is to determine the organisation of the unit that gave rise to it. In the last chapter the annelidan unit was described in its simplest condition as a linear free-swimming colony of gastræal units, the foremost of which perhaps were mature, while those which followed were buds diminishing in size from before backward. This was the homogeneous condition of the gastræal colony, and, before it could produce a new unit, it had to be integrated and specialised into an organism capable of building up colonies for a new period. Our experience of the earlier periods has made us familiar with the formula for the process of welding an aggregate into a complete whole; the clustering, fusing, and centralising of unit-organs and the joining together of unit-tissues to form the definitive organs and the more elaborate centralised system of tissues of the new unit. The first three units have, as we have seen, all been perfectly centralised.

The one important organ in the gastræal unit was the digestive cavity, and the one important tissue the neuro-muscular sheath of filaments which had to become felted together in consequence of the crowding of the nuclei between the outer surface and the cavity. In

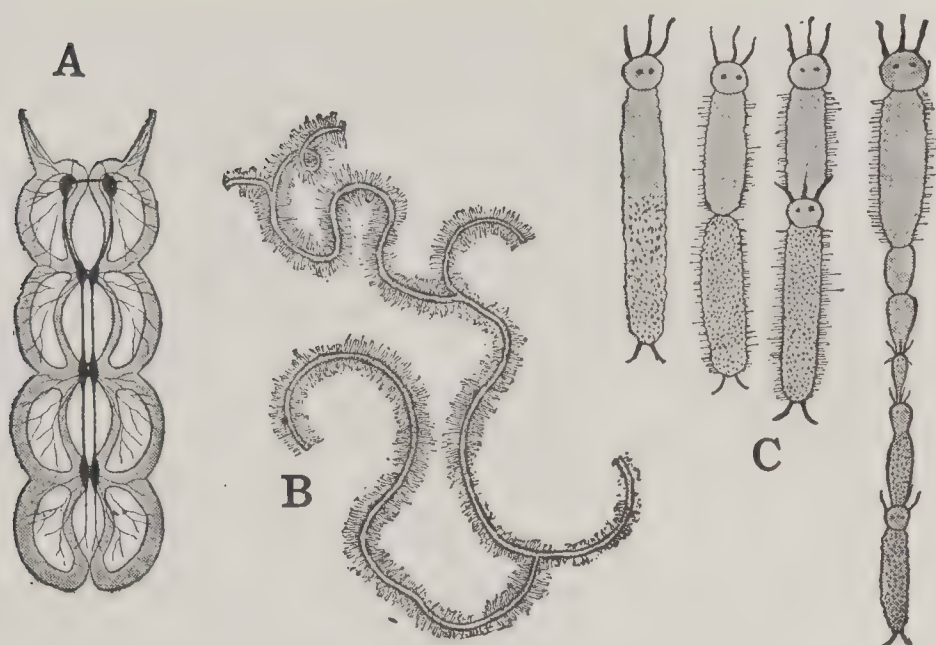


FIG. 46

- A. Diagrammatic representation of the horizontal longitudinal section of a primitive Annelidan colony. The separate gastræal units of which it is built up are still indicated by constrictions; the alimentary canal runs from end to end of the body and has an opening at each end. A series of "mesodermal" cavities appears on each side of the alimentary canal. These cavities represent the spaces which have arisen in the neuro-muscular system and which divide the latter into a layer of muscles for the alimentary canal and another for the outer wall. The nerves have separated out from the muscles and take the form, in each segment, of two swellings placed anteriorly and joined together by "commissures." The pairs of nerves, besides sending ramifications among the muscles, are joined by two longitudinal commissures, so that the whole series of swellings form together a ventral chain (called the "ladder nervous system" of the annelids). The mesodermal spaces collect the waste products from the muscles and nerves and communicate with the exterior by ciliated channels (nephridia or primitive kidneys), through which the waste is drained off. These channels are not shown in the diagram.
- B and C. Two forms of the colonies that could be produced by such a primitive annelid. B is a branched colony and C one produced by budding in linear series of indefinite length. The buds are no mere coelenteric segments, but represent annelidan units.

the specialisation of the linear free-swimming aggregate formed by the gastræal unit we naturally, therefore, look for modification of the digestive cavity and actually find that the cavities of all the component units run together to form one continuous alimentary canal for the whole complex (Fig. 46, A.). This, when the posterior opening is acquired, becomes an efficient organ for dealing with the problem of nutrition, an organ far more efficient, indeed, than the simple blind sac of the gastræa, inasmuch as the food now enters at one end of the body and the waste is ejected at the other; a continuous stream of food thus passes over a much extended digestive surface. Accompanying this linking up of the alimentary cavities, we find a similar joining together of their neuro-muscular sheaths or walls, which unite to form one common tubular system for the new organism. In typical annelids, this common sheath, while retaining traces of division into the portions contributed by each unit, develops into a very large and powerful neuro-muscular system, especially in cases where the animal becoming, by normal growth, too large to propel itself by cilia, adopts the more effective method of locomotion by serpentine movements of the whole body.

An organism built up in this way could not possibly long remain undifferentiated. The same muscular layer could not continue to function for the outside wall with the motions proper to it and for the alimentary canal, which requires its own movements for dealing with the stream of food. Hence a very early differentiation, the original muscular layer splitting into two muscular layers, one for the energetic movements of the body wall, the other for the special movements of the digestive canal. This splitting of the layer

would lead to the formation of internal spaces (the mesodermal cavities) between the two sections. The differentiation of the muscular layer into two layers would also necessitate the separation of the nerves from the muscles in each segment, thus giving rise to separate segmental nervous systems, which would not interfere with each other's functions. The original uniform muscular sheath of each segment, being differentiated into a nervous system and a muscular system which were morphologically distinct, must still remain a physiological whole for each segment. A number of such segmental systems united together, muscles to muscles and nerves to nerves, ensured the efficiency of the free-living askeletal organism.

Within and out of the solid wall between the outer surface of the body and the alimentary canal of the gastræa, a highly complicated neuro-muscular system was thus, sooner or later, developed and, in order to keep this system efficient, some mechanism for removing the waste products was necessary. Waste matters would be the inevitable result of the activities of the muscles and nerves, and would accumulate in the "mesodermal" spaces of the segments. Small canals opening at the surface of the body developed as the first beginnings of the kidneys of higher forms.

From this stage onward, the "mesoderm" becomes an important morphological region of the body. Its origin was perfectly natural, but the rigid morphological value which has been assigned to its lining epithelium is quite artificial. An organism whose structure is essentially a continuous linin network with nuclei suspended on the filaments has special centres of vital force ready to line any cavity opening near them and can produce an epithelium where none was present

before.¹ Epithelia thus arose *in situ*, in direct response to physiological needs.

The specialised form derived from one of the homogeneous aggregates of the gastræal period may be briefly described as follows:

1. It was a powerful free-swimming organism capable of chasing prey at great speed through the water.

2. Machinery for the capture of food was conspicuous by its absence, the prey being originally seized by the mouth alone as the animal rushed through the water.

3. There was no hard, protective covering to prevent the organism from being sensitive to the environment and if, in view of the flexible layer of chitin that spread over the skin, we cannot say that its nerves were everywhere exposed, it is clear, from the fine structure of the external chitin, that it would do little more than protect the tips of the sensitive filaments which penetrated it and built it up.

4. The nerves became specially developed at the anterior end of the body and early began to show signs of differentiation; some became complicated masses of pigment and built up eyes; others became auditory, others olfactory, and tactile organs also attained great development. These differentiations caused special concentration of the nerve-centres in the "head" or first segment for the co-ordination of the stimuli received from the sensory organs.

The annelidan form which we claim as the unit of the fourth evolutionary period was thus not only sensitive from end to end but, with its differentiated sense organs,

¹ Pt. I, p. 131.

was capable of instantaneous and powerful response to a wider and deeper range of environmental stimuli, the extent of its environment being vastly increased by its powers of locomotion. In its responses to stimuli, it would act as a whole, though its length would tend to endanger perfect organic centralisation.

This primitive annelid, however probable, is, I admit, so far hypothetical, but I believe that some evidence can be adduced in favor of its existence. In an enigmatical animal, apparently a worm, which has puzzled and still puzzles zoologists—*Sagitta* or the Arrow-worm—we find the chief characteristics of our hypothetical form. *Sagitta* consists of three segments, and its nerve plexus forms one large concentrated mass in the middle of the ventral half of the body. It darts with lightning-like rapidity after its prey, which it seizes with a mouth armed with the simplest conceivable chitinous bristles, bent into jaws. This form appears to me to be the annelidan unit specialised and perfected, and seems to bear to that unit the same relation as the sea-anemones to the *gastræa* and *Actinophrys* to the cell. It is quite possible even to trace its specialisation and to see why it departed from the primitive form. It evidently wandered off into the deep water of the open sea, which it still inhabits and where it had no wide range of environmental variations to trouble about; to seize prey and escape from foes was the sum of its life-activities. The primitive annelid, on the contrary, remained close to the shore and, in the thick of its struggle with a tangle of plants and a vast concourse of animal organisms of all sizes and armed with all kinds of weapons of offence and defence, it required to feel its way and to be wary. These differences of life-habit fully account for what chiefly needs elucidation,

the different specialisation of the nervous system in the two organisms. By the welding of its nervous strands into a single complete, co-ordinated system with one large central mass near the middle of the ventral surface, the Arrow-worm attained a centralisation rivalling that of the cell and the gastræa, but differing from that of the annelidan unit and bearing unmistakable witness to possibilities of fusion of the segmental systems into one. In the annelidan unit, which was destined to raise life to a higher level, the chief centre of co-ordination arises in the head and becomes the foundation of the brain of all the higher forms. This centre is not needed solely, as in the Arrow-worm, for concentrating all the active forces of the body upon the seizing of prey or escape from a foe, but has a much greater significance and wider purpose—that of exploring the environment. There is no need to read a too modern and realistic meaning into the word “explore.” If the term “exploration of the environment” sounds somewhat fanciful in this connection, it will be found, as we advance, to acquire, by degrees, a very real meaning and one which becomes of almost the first importance for understanding the drift of the evolutionary series. Slowly but certainly we shall find that there is no advance in evolution except in relation with a progressively more extensive and more complicated environment. Hence the Arrow-worm, though probably the first of the annelidan units to become centralised as to its nervous system, remained stationary, chiefly, I believe, on account of the uniformity of its environment. If it ever tried to build up colonies, these were unable to survive.

The annelidan unit grows to its full size, that is, to

the full number of fully grown gastræal segments, and then it begins, as the earlier units did, to divide for the formation of its homogeneous colonies. Equal fission had to be given up, as we saw, even in the gastræal period, and to be replaced by budding. This change we traced in the stationary coelenterate forms, and in free-swimming forms it would seem to be even more imperative on account of the paralysing effect of fission while the process lasts. The very existence of the annelids was accounted for by the fact that the free-swimming gastræal units early began to bud at the hinder end, and any idea of the annelidan unit, a short string of free-swimming gastrææ together making a compact whole, dividing into two equal halves, is out of the question. Budding must therefore be thought of as invariable during this period and as being naturally restricted to the least differentiated, hinder end of the body. This is the rule in all the annelidan world, in which lateral buds would be inconvenient, at least for the creeping or free-swimming forms, though stationary forms might bud laterally and produce tufts.

Budding is thus the normal method of colony-formation in the annelidan period, and budding, to be consistent with our periodic formula, must mean, not the budding of fresh segments of the value simply of gastræal units, but the budding of entire annelidan units from annelidan units. And this, as we shall see by consulting Fig. 46, C, is exactly what takes place. Each bud is a young stage of a new annelidan unit.

And now what kind of colonies could be thus produced? Branching or tufted annelidan colonies are not numerous, but one of the most remarkable finds of the Challenger expedition was a branching worm living in

a hexactinellid Sponge; a small portion of this worm is shown in Fig. 46 B. It is possible, of course, that this is a case of secondary specialisation, but it is significant to find that it happens to be one of the Scyllidæ in which budding is still very pronounced, mostly in linear series. Dense tufts of worm-tubes are, of course, very frequent, and these tufts might have been produced by lateral budding or even perhaps by longitudinal fission with subsequent budding. We certainly find large compact masses of such tubes, both recent and fossil, side by side, as if their inhabitants were all alive at one and the same time. They might be explained as an organic colony, for it is not easy to imagine any animals choosing, if free, to live so close together¹; but the matter requires investigation.

Linear budding alone, however, could form efficient colonies capable of being welded into compact wholes. Of the existence of these there can be no doubt. That they were built up of annelidan units we know from the fact that the buds often appear with eyes and antennæ, and I do not hesitate to claim them as homogeneous annelidan colonies. We need not wonder that the processes of annelidan budding are now somewhat confused, because the annelidan unit itself grew by multiplication of the gastræal units of which it was composed, while the aggregate now grows by the multiplication of the annelidan unit. A double com-

¹It is worth noting that branching worm-tubes are not by any means rare; they are found associated with both Corals and Sponges. In some cases the worms themselves are known not to be branched (see Prof. Haddon, *Proc. Royal Dubl. Soc.*, viii, 1895, p. 344). But I have found instances of what appeared to be branching worm-tubes embedded in the heart of a rising and branching coral stem, an arrangement which is inconceivable except on the supposition that the worm also branched (see B. M. Catalogue of the Madreporarian Corals, iii., p. 145).

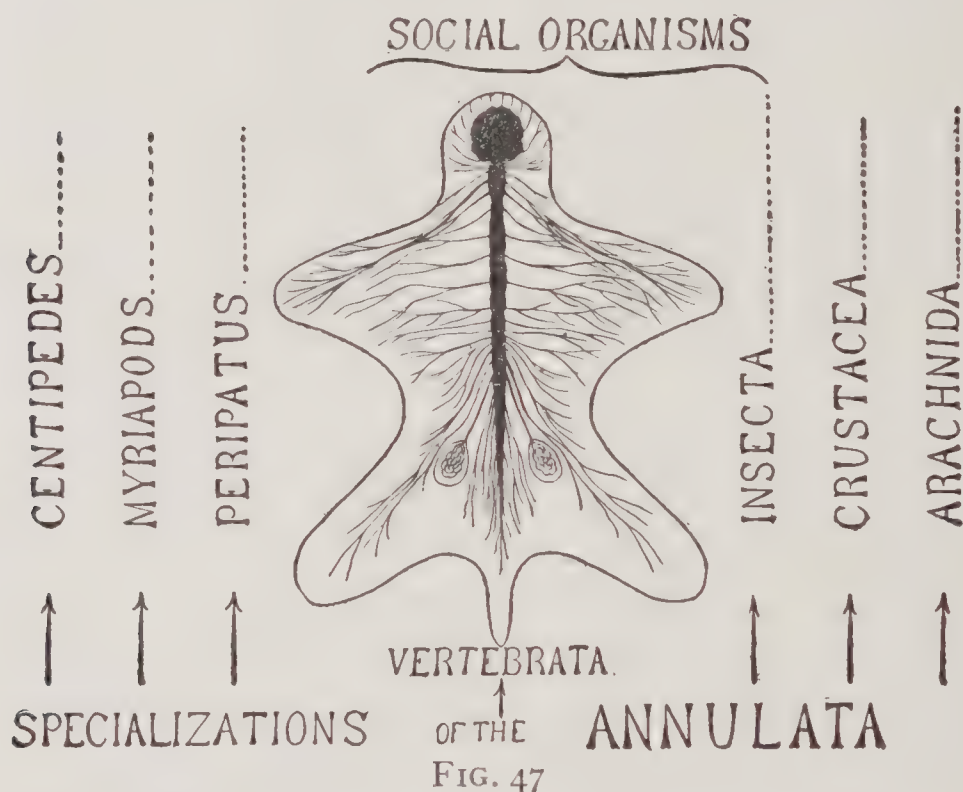
plication has to be kept in mind, and it remains to be seen how far a close analysis of the facts of these budding processes by experts, made in the light of this scheme, will yield confirmatory results.¹

We have now briefly to review the specialised organisms which resulted from the lapsing of the homogeneous aggregates of the annelidan unit into heterogeneity, in the hope of finding one capable of functioning as a new unit, and at first, as in the last period, we seem to look in vain.

If the reader refers to Fig. 47, p. 378, he will find, among the groups now generally recognised as having been produced by the specialisation of primitive annelidan aggregates, a vast number and diversity of animal forms. This is, of course, what we should expect, because the annelidan organism is far more complex than any unit that preceded it and, the more complex an organism is, the greater the number of varying factors it possesses with which to confront a greatly increased number of different environments.

¹ In an earlier sketch of the origin of these larger or colonial annelids (see *Annals and Magazine of Natural History*, vi, 1901), I regarded them all as having been produced straight away by the addition of gastræal segment to gastræal segment. I no longer think, however, that the lengthening process took place thus gradually and uniformly, but rather that it advanced in two steps, first, in period III, by the multiplication of gastræal units in order to build up the annelidan unit, secondly, in period IV, by the multiplication of the annelidan unit to produce the longer and more complex forms. It would, it seems to me, be easier to conceive of these already highly differentiated annelidan units combining to bring about the integration of the higher forms than of a long string of simpler undifferentiated gastræal units being able to do so. The class Vermes, however, contains so many strange forms, with such varieties and obscurities of segmentation, that several different lines of development and specialisation may be required in order to account for the phenomena.

Now the chief factor of an environment, *i.e.*, the one in relation to which organisms most frequently vary and become specialised, is the food supply, and it was no doubt this factor which determined the varied development of the descendants of the primitive annelids. They became specialised in connection with



Diagrammatic outline scheme of the higher Vertebrata so far as the nervous system is concerned. It is intended to show the extraordinary size and concentration of the vertebrate nervous system. The figure also indicates the glands enclosing those structural elements which are early set aside in the embryo, and until the organism is adult are withdrawn from active growth, being reserved for reproduction.

the food they required and with their method of obtaining it or of feeding.

The way in which three of the distinct groups represented in the diagram Fig. 47, the Crustacea, the Arachnida, and the Insecta, were derived from the annelids has been traced by me elsewhere. The annelid

ancestor of these three groups possessed "parapodia," which, however, were used in three different ways for bringing food to the mouth, the result being that the limbs in these groups became differentiated along three different lines.¹

In another paper,² I attempted to show that the complex organisation of the Vertebrata can be deduced from an annelid devoid of parapodia, which retained and perfected a more vigorous method of locomotion by means of serpentine movements of the body, a method that would have been hampered by parapodia and that necessitated a specially powerful body musculature. Leech-like forms may, I believe, be considered as the ancestors of the vertebrates,—forms which had to seize their prey with the mouth alone, as they met with it in their onward rush. The transformation gradually brought about by this method of feeding, so different from that of the Arthropoda, was traced by me step by step. A smooth, free-swimming form was pictured as earning the reward of great activity by catching and engulfing a large quantity of food. In a coelenterate, distention of the body by food-stuff need not greatly impede movement, but the distention of an annelid, whose locomotion depended upon serpentine movement, would be fatal to its efficiency, and modifications of the organisation would be necessary to avert the consequences of such enlargement of the alimentary canal. It was, I believe, these modifications which played the chief part in changing the annelidan organism into a vertebrate organism. The above theory, elaborated

¹ "The Apodidæ," *Nature Series*, Macmillan, 1892, and "The Comparative Morphology of the Galeodidæ," *Transactions Linnean Soc.*, vol. vi, pt. iv, 1896.

² "A new reading of the Annulate Ancestry of the Vertebrata," *Natural Science*, vol. xiii, 1898.

as an attempt to solve one of the burning questions of biology, the origin of the Vertebrata, is now unexpectedly confirmed by finding that the method of feeding attributed, in 1898, to their annelidan ancestor, is the same as that which characterises all the earlier forms that have succeeded in raising the level of life.

It is thus among the descendants of leech-like ancestors, I believe, that we have to look for a new unit of structure fulfilling all the requirements of a typical unit. The first of these, it will be remembered, is the concentration and centralisation of the forces of the organism. This centralisation was, as we saw, to some extent endangered by the length of the primitive annelid, a danger that was obviously exaggerated in the long colonies it built up, so that a return to concentration and centralisation seems absolutely necessary before another efficient unit can be produced. The difficulties in the way of such a return must naturally have been enormous and appear, in themselves, sufficient to account for the ages that elapsed before life was once more raised to a distinctly higher level. Some idea of the extraordinary duration of this annelidan period may be gained by recalling the fact that the Trilobites, which can, I believe, be shown to be specialisations of annelidan colonies, are among the very earliest known fossils.

The growing importance of the nervous system is clearly one of the chief characteristics of organic life as it increases in complexity. In the higher organisms of the annelidan period it is undoubtedly the nerve centres that are the centres of force. In order to be an efficient mechanism, no part of the organism must be too distant from the nerve centre; the whole consequently has to be compact. In the earlier annelidan colonies, a ventral

nerve chain runs along the whole length of the body, a condition obviously not in keeping with the concentration required in a unit of structure. But even in the Crustacea, the Arachnida, and the Insecta, we find a tendency to shorten the chain; it concentrates anteriorly in connection with the needs of the numerous limbs developed from the parapodia of the annelidan ancestor of these groups. In the leech-like, limbless ancestor of the Vertebrata, there was not the same need of a ventral nerve chain, but it was retained in dwindling importance on account of its indispensable visceral connections. In these forms, new nerve concentrations took place in the upper dorsal half of the body, the half in which the chief muscular tube was situated, and this resulted in the development of the dorsal nerve system and brain which form the peculiar specialisation of the higher Vertebrata. In the anthropoid Apes the nervous system at last attained a compactness rivalling the extraordinary concentration of the forces in the cell and the gastræa, and this character was combined with another of the typical morphological requirements of a unit of structure—great sensitiveness to the environment unimpaired by skeletal protective plates.

I would point out also that the activity and voracity which have distinguished all the units of structure and which seem to have reached their climax in the leech-like ancestor of the vertebrates, are of great significance. The presence, in each unit, of these characters indicates to my mind, most unmistakably, that while, in many organisms and notably in the plants, transformations of structure are passive reactions to the environment, the changes in the more energetic forms which lead the van of evolution have been directly due to an active *storming of the environment*

in order to obtain what the organism desires. This difference is clearly to be correlated with the development of the neuro-muscular system; as the nerves develop, the desires lead the reactions.¹

In the organisation of Man, the representative, after ages of differentiation, of the anthropoid Ape, we find all that is needed in a typical unit of structure, though on a far higher level of complexity than in any former case. In Man, also, we have the highest of the colony builders, for human societies are, as I hope to show in the sequel, colonies essentially serial with those produced by the earlier units of structure.²

¹ As the race in life belonged to those which were most energetic in the method adopted, it looks as if the development of nervous systems were the prize.

² Social life first appears among the vertebrates in the Insecta and it is a significant fact that a comparative study of the nerves of insects and arachnids shows almost every stage of the difficult process of longitudinal compression of the original long nerve chain. The nervous system of the Insecta was both complex enough and sufficiently co-ordinated to allow of the formation of social colonies, but their range of environmental stimuli was very limited, and they seem to have exhausted the possibilities of higher integration. Insect colonies seem, consequently, to have drifted to one side of the evolutionary advance. They are, in any case, not serial with the colonies we are considering.

CHAPTER XXII

THE FIFTH EVOLUTIONARY PERIOD—MAN AS ITS UNIT

HOWEVER interesting the earlier evolutionary periods may be to the biologist, the interest of this fifth period is both wider in range and of deeper import for, in it, the human race comes into view, runs part of its course and, if there be any truth in my contention that these periods repeat one another, is seen in the act of taking the next step in its further advance.

In spite of the protracted records of history, human societies are still in the midst of their evolutionary career, and can therefore, of course, be but very incompletely described by the human units of to-day; and, apart from this inevitable limitation of outlook, we are confronted, in this period, with difficulties unparalleled by any we have hitherto had to face. In the first place, the unit of the period, Man, is a vastly more complicated organism than the unit of any former period. In him, the nervous system¹ is more highly specialised than in any other organism. The large central system, which sends out nerves in all directions to the surface, supplies highly differentiated organs of special sense, by means of which Man *feels* the environment all around him, not only that which is close at hand, but that which spreads out for a considerable distance, and this with a completeness never previously

¹ See Chap. XI.

attained. The bird may surpass Man in vision, the bat in hearing, the horse, physically, in strength and speed, but in Man alone are the fine senses so co-ordinated as to give a coherent report of the environment and, consequently, to supply a guide for effective responses to a wider and deeper range of it than is accessible to any other living creature. It is this potential mastery of a very wide environment, by the aid of the concentrated and developed nervous system, that has given Man his unique position in the animal kingdom, and that has ensured his supremacy over the other products of evolution.

In close connection with this development of the nervous system in Man, we find a wealth of new forces which may be comprised under the term "psychic,"—forces now for the first time brought into prominence, though the rudiments of them must have been present and must have found some kind of expression in the earlier types of units. For instance we find a craving for freedom and self-expression on the part of the individual human unit, combined with a hunger to know and feel more, *i.e.*, to live a fuller life, which seems to have a counterpart in some of the profoundest instincts of organic life in its earlier stages.

And not only is the human unit more complicated in itself, but its environment is far more complicated than the purely physical environment to which the primitive orders of organic life adjusted themselves and still adjust themselves. Social life has created a new environment for which, again, the term "psychic" must be used. Consequently, the attainments that constituted the perfection of the simpler unit are no longer all-sufficient. These might be summed up as ability, on the one hand, to obtain a sufficient food-

supply and, on the other, to repel the attacks of other organisms; thus equipped, the earlier unit could storm and explore a certain range of the physical environment. But the human unit has to attain a condition of stable equilibrium not only with an external, material environment, but with a "psychical" environment. The more perfect, indeed, the adaptation of Man to his physical environment, the more insistent and imperative do the claims of the "psyche" become and, unless these are met, the human unit, however well equipped for responding to physical stimuli, seems doomed to decay. The roots of the many and various psychical demands within and without the individual unit have to be sought in some subtle domain of existence which eludes the ordinary senses that were developed solely with reference to the physical; the evolution of their expression can be traced in outline, but not their underlying forces. Some can be defined, others are but vaguely at the present time inspiring the poets, the artists, and the deeper thinkers. To mention a few in haphazard order (for their physiological relationships have still to be worked out) we find the thirst for knowledge, the love of the beautiful, enthusiasm for liberty and justice, and the craving for sympathy.

The difficulty of combining such physically and psychically complex units into organic wholes is obvious. The units of former periods, with their small nerve centres, had no individual impulses strong enough to disturb the harmony of the aggregate into which they became welded; they were comparatively easy to bring into line, and learned to respond very quickly to the stimuli sent through them from the surface of the whole organism. The human unit has not the plasticity and adaptability of those earlier units. Its complicated

nervous system is a storehouse of spontaneous impulses extremely difficult to subdue for the attainment of any harmony. Further, the stimuli received at the surface of a social organism, in reaching each unit in such a way as to be appreciated, are liable to an almost unlimited number of accidental variations; consequently, not only harmony but unanimity of response, which is essential to the gradual co-ordination of the functions of the social organism, are very difficult to attain.

But there is a more fundamental obstacle in the way of the fusion of the human units into morphological, organ-like groups which calls for full discussion and which we must attempt to remove before we can pass on to trace the rise of social life.

The units of all the earlier evolutionary periods, after multiplying by incomplete fission or budding, remained connected by the linin filaments of their protomitomic networks, their union being consolidated later by tissues built up by those filaments. The process of fission or budding which multiplied the early units merely divided their centres of force; there was no rupture of the fundamental network; that remained a whole. But, when budding became an impossible method of multiplying, owing to the size and complexity of the units, which made it difficult for them to keep together in groups and still more to become welded into compact wholes, sexual reproduction took its place and, in this process, the continuity of the network must of necessity come to an end as soon as the young of a new aggregate are born. Each new unit is physically a separate entity, and how is it possible for such distinct units to become welded into a colony?

In facing this serious difficulty and in trying to eluci-

date it, the universal presence of the protomitomic network has to be kept clearly in view and it must also be borne in mind that the fundamental network of every organism is, essentially, an undifferentiated nervous system¹ and that stimuli are conveyed by this system through the organism as through a continuum. This being so, the chief points to be emphasised may be tabulated in the following way:

(1) The protomitomic filaments which, in former periods, have been at the base of colony-formation, and have supplied the principle of the cohesion of the units are, essentially, nerves.²

(2) It is not merely the fact that the nerves are physical strands which enables organisms to cohere and to become compact wholes, but the fact that they carry stimuli.

(3) It is the stimuli which travel along the nerves to the centre, and are then dispersed so as to bring about the necessary responses, that are the *essential* factors in the evolutionary process. Indeed, it is impossible to account for the welding of a diffuse colony into a compact one unless by assuming that the whole organism feels and endeavours to react as a whole to each stimulus.

(4) The physical nerve strands, consequently, are not the chief elements in the integration of homogeneous aggregates; it is the stimuli that are the indispensable factors. These must be communicable from unit to unit, in order that the units may endeavour to respond together. This, *with or without physical fibres*, is the sole condition of colony-formation and integration.

¹ See p. 189.

² See Pt. I, Chap. XI.

(5) Since the social aggregate we now have to consider, the only aggregate which this fifth evolutionary period can produce, is without physically connecting nerve fibres, the stimuli have to pass from unit to unit in some other way.

Treating the subject now concretely, let us consider the case of mother and child. Although they become physically severed at the birth of the latter, they still continue to be both physically and psychically interdependent; though physically separated, we may say that they are not "organically" separated.¹ When the violent rupture of the filaments² takes place, their synthetic functions find a new outlet in a plentiful secretion of milk; their nervous functions, also apparently dammed back, start an agitation in the nerve centre—an agitation so violent as to affect the whole frame, causing it to express concern, protecting anxiety, and impressive tenderness, all those nervous or psychic affections, indeed, that are usually summarised in the word "Love."³

The physical and nervous interactions that took place *in utero* are thus but momentarily interrupted, and are resumed on a higher plane, as it were. From having been unconscious and automatic, the connection between mother and child becomes an object of con-

¹ I am here reading a fuller meaning than usual into the word "organic," a meaning that may be illustrated and explained by noting that, however real such physical attractions or repulsions as have psychic counterparts (*e.g.* loves and hatreds) may be, their counterparts are just as real (see p. 392).

² Not the original filaments that bound the egg to the complex of which it was a part, but the secondary filamentous connections established during the passage of the fertilised egg through the uterus.

³ "Love is an affection of the mind" seems the only possible physical analysis.

sciousness, at first to the mother alone, but later gradually to the child also. In the mind of the mother, the feelings of love struggle hard to express themselves to the child as the foremost object of attraction in her environment, and the child is affected by a feeling of desire for the mother which it tries to express. The effect of this agony of "expression" on the part of the mother becomes evident in a language of caresses and sounds which may or may not take the form of words. But is the nerve agitation spent entirely in these indirect ways? May they not be regarded as merely collateral and incidental accompaniments of some real psychic influence which continues to pass between the mother and child across the space now intervening between her and the object of her love? Though nerve action figures largely in all the past evolutionary history, there has not, until now, been any question of nerve stimuli except as physical agitations in immediate conjunction with physical nerve fibres. And, even now, we are not claiming that nerve impulses exist quite apart from nerves, but the question raised is whether such psychic impulses cannot be transmitted through the intervening medium, so as to start psychic impulses in an adjoining but distinct nerve complex. If such direct transmission of psychic impulses, which, of course, is quite distinct from the indirect method of transmission by means of sounds and signs which seems so far to have monopolised human attention, could be established, it is obvious that we should have discovered a force that would serve the purpose of welding units together into a colony, even though those units were physically free and detached.

Here, then, we seem to be on the track of forces that can bind the units of a human aggregate together quite

as strong as, though perhaps more elastic¹ and variable than the physical fibres which united the homogeneous aggregates of the earlier evolutionary periods. This uniting force has two aspects, a physical and a psychical. In the case we have been considering, that of mother and child, the mother's desire for the child is more psychic than physical, that of the child more physical than psychic. The physical and the psychical seem to be counterparts of one another, but when the physical ceases, the psychical may persist.

A social aggregate may be said to arise in a similar way by the clinging together of separate human units owing to the fact that the physical attractions of unit to unit have their psychic counterparts which tend to persist like invisible nerve fibres. We seem here to have an organic parallel to the earlier aggregates that were linked together by actual physical nerve fibres. A compact organism is in each case the result of the process of welding the units together and stimuli received at the surface run through the whole, which gradually learns to respond as a whole.

In trying to show how stimuli are transmitted from one human unit to another, I am well aware that I am treading upon slippery ground, for I am dealing with the psychic aspect of the stimuli. Now, though matter is, in reality, just as mysterious as mind for us, we have, in dealing with the physical, a kind of scaffolding raised upon rigid sequences that we have been able to establish, and along this scaffolding we can tread more firmly than on anything that has so far been

¹It should however be admitted that the elasticity of the connecting filaments of an embryo is shown to be considerable by the well-known experiments which involve the flattening of a blastosphere without rupture of the filaments and consequent separation of the individual blastomeres.

built out into psychical regions. Consequently, in any such discussion as the one we are now engaged in, it is well to advance as far as we can along planks attached as firmly as possible to the physical scaffolding. We are still, in this way, on firm ground when we speak of the possibility of stimuli passing from unit to unit in a social aggregate by some indirect method of transmission. The mother, longing to express the stimulus brought to her by the sight, sound, or touch of her child, the scout who has caught sight of an enemy stealing close to the camp he is guarding, are both suffering an agony that they long to express. Now, the simplest indirect method of expression is of course that of gestures and sounds and, in such a large complex organism as the human unit, where the stimuli are extremely numerous, this method has, in time, developed complicated languages capable at their best of conveying many even of the subtler phases of mental condition from one unit to another, although we are ever conscious that, for the expression of our deeper thoughts and emotions, our words and gestures are little less than futile. So far as I can see, there need be no end to the evolution of this method of utilising physical and psychical energy. As knowledge increases, language gains in subtlety by the continual addition of new words expressing finer shades of meaning; it has long been assisted by writing and printing and is now further aided by the telegraph and the telephone. These are all psychical facts, showing that the mental conditions are continually communicated indirectly from one human unit to another and thus function morphologically as bonds which now not only hold the human aggregates together in compact organisms, but continually tend to draw the units closer

together for the ultimate integration of human societies.

Now, even in the far simpler aggregates of the earlier evolutionary periods, the essential co-ordination and integration are only possible through the free transmission of stimuli, though, in these simpler cases, we are under no necessity to characterise the stimuli as they pass from unit to unit by any such names as "joy," "fear," "love," or "hate." The fact that we have to use such words to describe the stimuli that affect the human unit is significant. These are by no means empty words, nor do they refer to the mere physical excitements of the nerves which involve a certain number of subtle chemical changes in the substance of the nerves. The names seem to indicate differentiations of some medium which, though obviously associated with the physical agitations of the nerves, is yet not that in which these physical agitations occur. We may say this without fear of falling from our physical scaffolding, if it be clearly understood that the word "medium" is purely figurative. We are perhaps safer if we use the word "psyche" instead, since that does not commit us to any opinion as to how the psyche is to be imagined.

Love and hate are real states or conditions and, so far, we find that they can be conveyed from unit to unit indirectly by means of gestures and sounds which eventually developed into language. Common loves and hates thus conveyed are among the binding forces knitting the units of the human aggregate together. But there must have been early ties binding the units before these gestures and sounds were elaborated into intelligible forms, and we may well ask whether nerve excitements were then quite incommunicable

from unit to unit. This seems so very improbable that I cannot refrain from discussing whether, in the absence of any physical connections between the units, there may not be psychic connections which have no existence in the physical or three-dimensional environment, but do exist in some psychic environment. Here, I admit, we are leaving our physical scaffolding. Let us see, however, how near we can keep to it so that, at any moment, we can grasp it. So long as it remains within reach, we shall not be without support.

The permeation of a crowd by the same emotion is a familiar experience, indeed the transference of emotion from one human being to another is of such common occurrence as to attract little attention. Instances of thought transference, again, come within the almost daily experience of many people, although these phenomena are totally unknown to perhaps the majority, probably from lack of the observing faculty, and are consequently discredited by them. It is a common experience, for instance, that the thought of a friend seems to well up in the mind suddenly, in the sense that it was not led up to by any previous train of ideas, and is frequently found to be connected with some action on the part of that friend, such, for instance, as the writing of a letter relating to oneself, or even the mere intention of paying a visit. There are, further, innumerable records of agonised thought at the moment of death or of imminent danger having been flashed into the mind of some individual miles away. Not only is the fact conveyed but often some, mostly incoherent, details of the real or threatened disaster—details explained when the full report arrives.

It is not always the intensest thoughts that are transmitted; those who experience the phenomenon

are frequently struck by its curious haphazardness. Trivial thoughts or incidents quite irrelevant to the serious current of one's inner life flashing across from mind to mind are very common, and are usually spoken of as cases of two people thinking of the same thing at the same moment. There can be no doubt that vast numbers of human beings have had and have such experiences, though so irregularly as to suggest that those of which they became conscious are but a selection of a vastly greater number which fail to attract attention.

Now, it seems to me that the affirmation of so large a body of human experience cannot be dismissed unceremoniously, still less now when we might legitimately ask whether the morphological sequence of our evolutionary series does not supply a kind of basis which, if itself established, is strong enough to render such phenomena not only possible and probable, but almost certain.

In addition, then, to the indirect transmission of thought from unit to unit of the human aggregate, I claim that there is some positive evidence and much reason for believing that such stimuli have had, from the first, some inherent power of flashing directly from unit to unit and of being transmitted in this way through the human aggregate. We are still far from knowing the laws that govern this process; it is, however, enough for us here that it occurs at all.

Psychic phenomena have thus, in the fifth evolutionary period, come to the aid of evolution. Using terms already familiar to the reader, I may say that, on the failure of the primitive linin network to embrace and tie the human aggregates together, the psychic counterparts

of the nerve energies have become the chief factor in connecting the units and have since, like the purely(?) physical nerve energies of the colonies of earlier periods, been welding the aggregates more and more closely into organic wholes and, consequently, as psychic phenomena, have been taking a continually greater part in the life of the aggregate.

When we come to deal with the colonies built up of human units, consequently, we feel justified in postulating that, though accidents of environment may have tended to foster association in some and to destroy it in others, yet the principle of association has been instinctive and organic, since the colonisation of human societies belongs to the series of colonisations which have been such conspicuous factors in bringing about organic evolution.

This point is very important and adds an element to the science of sociology which is much needed. Without it human societies would have to be regarded as more or less fortuitous aggregates of individuals who are slowly learning to co-operate.¹ To speak of these as organic units has hitherto been but a picturesque hyperbole which any one might deride or deny. But, if it be understood that human societies are and, from

¹ It has often been said that the discovery of the advantages of co-operation and union over isolation was the force which first started human societies. I do not think this quite a sufficient statement; it is only part of the truth. The impacts of the environment are quite as likely to scatter and disperse any mere accidental aggregation of units as to unite them and, once scattered, there would be no force to bring them together again in the absence of some inner bond such as that I have been postulating. Given a psychic bond tending ever to become more complex and, if I may say so, more psychic, dispersive forces could act only temporarily, whereas such welding forces as the obvious advantages of mutual aid and general co-operation would be of permanent value.

the first, were as much organic products as were any of the primitive Metazoa or colonies of cells, sociology becomes at once primarily a morphological science, and all past history can be described in morphological terms.

This claim is a necessary result of our rhythmical law. All former colonies have lapsed into heterogeneity through the interplay of organism and environment; the organisms settling down in various directions as organic wholes to different environments and, as wholes, equilibrating with these environments. This must also be the case with human societies; they too have to settle down as organic wholes and they too, like the colonial aggregates built up by earlier units, have to become differentiated, though, as we shall see, not quite in the same way as in former periods.

But before attempting to describe the earliest stages in the integration of the human aggregate and to trace the later phases of its differentiation, we must pause to consider more closely this new and mysterious factor, the "psyche," which has now taken up such an important position on the horizon, and which has to be recognised as one of the most vital elements in any discussion of Man or of social life.

CHAPTER XXIII

THE VITAL FORCES—THE PHYSICAL FORCE OF LIFE AND ITS PSYCHICAL ACCOMPANIMENT

THE reconstruction of the fine texture of protoplasm sketched in Part I, which explained it as a continuous linin-chromatin network, has enabled us to cast the organic framework of evolution, for the first time, into some definite and intelligible order. We have been able to detect the part played by colony-formation, and to obtain a glimpse of Life coming up silently through the ages as a vast procession which is now sweeping past with the roar and bustle of the present and disappearing into the silent future.

This procession has had for its object the increasing size and complexity of the linin-chromatin network which becomes a more and more powerful mechanism for interaction with the planetary environments, and yet is, at the best, of course, frail enough in the scale of cosmic forces. Until now, we have been in absolute ignorance as to the meaning of this advance of life. The prevailing doctrine of evolution has shown us that the present level of life has only slowly been reached, but of what that level is and of the aim and direction towards which mankind is trending, it has told us nothing. But this condition of absolute ignorance seems to give place to some glimmering of knowledge, as our evolutionary scheme reveals an order in the

procession of life, a revelation which cannot fail to be instructive, though time and study alone can show the degree of our enlightenment.

It is now possible, for instance, for us to state, with approximate accuracy, the step in the ascending scale of life on which we are standing and, what is more, we can dimly outline the next step in the immediate future. Human societies are seen to be at present in the middle of their special period. The unit of this order of life has multiplied and has slowly built up vast colonies or social aggregates which are all, without exception, settling down to their several planetary environments. In all former periods, the integration of colonies into organic wholes was carried out successfully and, no doubt, it will be so carried out again. In the earlier periods, however, the stimuli were always transmitted from unit to unit automatically through continuous nerve fibres, from one end of the aggregate to the other, and the whole learned to *respond as a whole*. But in the present period the conditions have changed, and the stimuli have now to pass from unit to unit without fibres to carry them. Some of these stimuli, we have reason to believe, pass directly (telepathically); these are broken and, until corroborated, uncertain messages. Other stimuli filter through indirectly by means of gestures and sound, and even here there are elements of uncertainty in the transmission of the message. A further difficulty arises from the fact that each unit is a large, powerful complex which, as it were, feels the stimuli for itself and only passes them on after some delay, seldom or never exactly as they were received. The integration of the human aggregate has, therefore, necessarily been a long and difficult process. A new and mysterious factor,

the "psyche," has appeared upon the field and becomes more and more evident as life rises to higher levels, taking a prominent part in binding the units together, so that the process, formerly explicable in purely physical terms, has now to be considered from a new point of view; and a closer analysis of what may be called the "forces of life" seems at this stage to be called for.

What are the vital forces that have made us what we are, and are driving us forward? Some such forces there must be and our evolutionary scheme will surely throw light upon them.

Any student who has hitherto sought to unravel the forces of life has met with insuperable difficulties. In the most elementary forms of life, as in the higher and more complex, the so-called vital functions have proved insoluble, for they have baffled our finest methods of chemical and physical analysis. Perplexing as they are in themselves, they are rendered still more so by the fact that, hovering near them and around them and, for all we know, inextricably intermingled with them, there is an element which is neither chemical nor physical, a force *sui generis* which we call "psychical."

Students of this subject are divided into two camps. There are, on the one hand, those who, while admitting that there are superficial phenomena explicable by chemistry and physics alone, appeal, in most cases, to some active intermixture and interference of the psyche; they postulate some "vital force," to which the phenomena of life, physical, chemical and psychical, may be referred. Those of the other camp, on the contrary, claim that the phenomena of life are of two distinct

kinds, those due to chemico-physical forces and those due to psychical forces. Many chemico-physical problems have, they say, been solved without appeal to any psychic element, and they maintain that we are not justified in appealing to any psyche to help us except in admittedly psychic problems. Any special "vital force" is repudiated by them as an unwarrantable hypothesis, which may, perhaps, clear the air for a moment, but only by creating confusion of thought below the surface.

Into this conflict between the "vitalists" who cannot get beyond the empty term "vital force" or tell us more nearly what they postulate, and the so-called materialists, who cannot prove a negative, I should hesitate to plunge did I not believe that our evolutionary rhythm supplies us with a substantial contribution towards the solution of the problem at issue. For, from end to end of our rhythm, we find one stupendous physical force, the demonstration of which is so simple as to be obvious, and this, I believe, has some claim to be regarded as *the physical force of life*.

The first and most obvious exhibition of such a force that we find in our evolutionary scheme is yielded by the periodic outburst of the homogeneous aggregates. Such an outburst begins every period and is the cause of it. It may, on the face of it, be assumed that all these outbursts are due to one and the same force, the nature of which, so far as we can make it out, can be arrived at as follows.

Every period of our rhythm is started by the fact that some complicated chemical compound, more or less highly organised as to its reactions with its medium, has the power of growing by assimilating to itself from that medium the materials needed for its con-

tinued existence. At a certain stage of growth, internal strains are set up which compel the organism to divide into two. Some law of its own constitution, of which we are quite ignorant, compels it first to grow till a certain condition is reached and then to break up into halves, each of which again starts growing. We may provisionally describe this as a regular alternation between a *force of aggregation* (growth by assimilation) and a *force of segregation* (division of the whole into two). The origin and secrets of these alternating forces are, I repeat, lodged in the ultimate mysteries of matter.

That this complex of forces—a force of aggregation alternating with a force of segregation—has a strong claim to be the vital force of life on the physical side, is supported by the fact that it not only causes those tremendous outbursts of energy which begin every new evolutionary period by building up vast numbers of homogeneous aggregates, but that it is also the active force which drives life forward through period after period. For it is this same force which, after building up the homogeneous aggregates, causes them to multiply by sexual or asexual reproduction, and thus to shower down countless generations of individuals and colonies upon the planetary environments with which they have to equilibrate if they are to survive. Indeed, we can sketch the history of each evolutionary period in terms of the activities of this force. Myriads of forms are produced by the complete division of the unit; myriads of colonies are produced by incomplete division, and the numberless organisms that result from the welding of these colonies continue to multiply by ordinary reproductive processes through all subsequent time. One or two of them ultimately succeed in

becoming new units, and burst out again into colony-formation and begin a new period.

This force of "doubling division" which lies at the bottom of all colony-formation, all sexual reproduction, and all growth (true growth by assimilation of new matter being part of the process) is universal, from end to end of evolution. Does not this universality alone establish its claim to be the vital force? And when we come to consider its extraordinary activity, both intrinsic and extensive, the matter seems to be placed beyond all further doubt.

By intrinsic activity, I mean the marvellous processes that come to light in the phenomena of division.¹ The cell, for instance, is already a complex tangle; it is an intricate network of linin threads, with clusters of chromidia scattered within it in an order too complicated for us to comprehend. Nevertheless, this tangle is regularly and rapidly divided by some mysterious and irresistible force; the linin filaments are lengthened and split longitudinally, and the chromidia suspended upon them are halved. So that, where there was one three-dimensional tangle, there are now two, interlocked with one another in a way which it would pass all the wit of man to disentangle and separate without rupturing the threads. And yet, in the division of every cell, a marvellous rearrangement of the whole tangle takes place, so that the two come apart, and then, on parting, either resume their normal forms or perhaps merely prepare again to divide! Still more bewildering, if there can be degrees in complete bewilderment, is the division of the gastræa, and the attempts of division of even higher forms such, for instance, as that

¹ See Pt. I, Chap. XIII, and Fig. 39 A-E.

which I believe is made by whole coral colonies as colonies.

The enormous powers of multiplication of many of the minute organisms exhibit the activity of the force in another manner. A most striking example of this power was witnessed by me on the river Volga near Yaroslaff. The great river ran green from shore to shore for a whole week, stained by one kind of thread-like alga. For over a thousand miles, the waters of that mighty river were filled with countless multitudes of this minute plant which rapidly perished and sank as sediment into its mud. Here we have this extraordinary force of segregation which I regard as one aspect of the force of life producing, in a few days, a perfectly astounding phenomenon.

And this one complex force which is written large across the face of our evolutionary framework is no mere abstraction about which we merely speculate, nor is it a force which, having produced the forms of life, is now quiescent. It is still constantly at work at the present moment, hurrying on the vast array of living forms, either merely to produce themselves in ever renewed millions, or to advance to stages of greater complexity. Each one of us human beings, the units of structure of the last and greatest of the evolutionary colony-formations—human aggregates—is being hurried on by it to our individual and collective culmination or elimination. And this force is never quiescent so long as the conditions necessary to its activity are present. Small organisms, it is true, pass through periods of temporary quiescence or “suspended animation,” as it is called, brought on by drought or cold. Or, if we take an example nearer to ourselves, there is a temporary quiescence of the life force in the

sperm-mother cells and in the eggs of the female. These latter may be regarded as small portions of the body temporarily (*i.e.*, during the general growth of the body) rescued from the action of the vital force and sequestered in the sexual glands. Here, so far as active growth is concerned, they remain quiescent¹ until, when the whole body of the adult is ripe and its growth has practically ceased, the eggs are ready to start growing from where they left off. Then, after fertilisation, the microscopic egg develops into some comparatively gigantic form with astonishing rapidity, a phenomenon quite as startling in its way as the multiplication of the alga in the Volga and still more startling in the fact that the organism produced exactly repeats, not some extremely simple algal parent form, but a highly complex organism which can only with difficulty be thought of as ever having been a single cell.

The sperm-mother cells of the male also remain quiescent during growth, but when the adult condition is reached, this same vital force of division continues for forty years in full play producing the male elements of reproduction.

And not only does the regular normal growth of all growing things testify to this alternation of aggregation and segregation, but it is exhibited equally clearly in certain abnormal processes. The terrible scourge of cancer, for instance, results from so many sporadic outbursts of this same force, escaped from control and destroying the bodies which, under the guidance of heredity, it had first normally and regularly built up.

I would here point out that this physical force has come to light and is seen to hold such a prominent

¹ See p. 260 for the functions which may be provisionally attributed to them.

position chiefly because we are now able to arrange evolutionary phenomena into a series with a definite and intelligible order. It is this order, indeed, which reveals the force. The importance and mystery of the phenomenon of doubling division had not by any means been overlooked by biologists but, so far at least as current biological teaching goes, no adequate appreciation of the part it has played in evolution has hitherto found expression. Its appearance, lurking somewhere at the bottom of the well of life, has naturally aroused the keenest interest. But, surely, never has it appeared in such splendour as now when the great sweep of our evolutionary scheme, starting from the growth and division of microscopic molecules, is seen advancing in great waves through the ages. Peopling the planet with living beings and making ever new and larger conquests of the planetary surface, this great life force sweeps onward, even reaching out beyond the planet itself, not only weighing and measuring other celestial bodies, but also penetrating, as we shall see, that subtle region that belongs especially to the psyche, the fundamental laws of which have been unknown to us except as an abstraction called "truth."

The discovery of the vital force of physical life has been a comparatively easy task, and the force, however complex in its ultimate molecular analysis, is comparatively simple. But the "psyche," as we have called its psychical accompaniment, has hitherto been little more than an abstraction. Since, however, our feelings of pleasure and pain, of anger, hate or love, are real, we have here to treat of the psyche as a reality, though not one of those realities that can be submitted to the usual tests of the three-dimensional environment we

inhabit, weighed, for instance, or measured. It has, however, one attribute in common with ordinary physical phenomena, and that is that it can be *felt*. Weighing and measuring are, of course, only highly complicated forms of feeling (we feel the scales and we see the register), so that, ultimately, physical and psychical phenomena seem to have the same reason for being regarded as realities. Both alike are states of consciousness. But, in dealing with psychical matters, we are at a certain disadvantage for, instead of a definite language such as has been developed in connection with the common physical phenomena, we have, for the scientific treatment of psychic phenomena, nothing but a loose and vague terminology.

In trying to investigate the psychical accompaniment of the life force, we must follow a method similar to that just employed in searching for the physical force. We have to gather all we can about the psyche first from our evolutionary rhythm, noting its actual appearance in our fifth period, as well as all its appearances in us associated with our life processes and, wherever similar processes are revealed in former periods, assuming that the psyche was present there also. The task is one of great complexity; at the best we can but attempt to force a rough path through the tangle of facts which, like clinging briars, claim our attention. The inherent difficulty is increased by the fact that a morphologist, without expert knowledge of psychology, is here compelled to trespass upon the domain of the psychologist. The results obtained must therefore be regarded as merely provisional.

But before we can make any start in selecting the psychical from the physical we must be quite clear that both are real and distinct, and that, however

inextricably they appear to be interwoven, it is possible to separate them out for distinct analytical treatment. This preliminary discussion is of itself intricate, yet it is necessary before we can advance a step.

There can be no doubt that this psyche which shows itself under so many aspects, every one of which can be analysed into some complex feeling either of pleasure or pain or of both, has become a factor of social life almost, if not quite, as obtrusive as our physical organisms and surroundings. Each human unit during his lifetime experiences progressive transformations in relation to it. At, and for some time after, birth, the life of each individual appears to be almost purely physical but as it advances, the psychical element develops and, normally, continues to claim an ever larger share in the life activities, remaining active even when the physical has obviously begun to decay.

So real, indeed, is the psyche in spite of the fact that it is nothing to eat, to weigh, or to measure, that there have been strange philosophies concerning it. Some have been so astounded at its marvellous presence, its diversity, and the difficulty of thinking of it and physical life as linked together, that they have been led to deny the existence of matter, *i.e.*, of the physical world, altogether. The psyche is to them the only reality, while, as a counterblast to this, many, especially students of the physical world and of the earlier phases of evolution, have been so impressed by the splendour of the physical sequences, which seem to require no psyche to account for their phenomena, that they have been led to deny as emphatically that there is any psyche, except perhaps some subtle force, which will one day be resolved in terms of physics.

With neither of these views am I in sympathy.

What we have to do is patiently to analyse the phenomena of life, with the object of discovering, if possible, some definite and intelligible conception of what the psyche is, of the nature of its association with the physical, of the part it plays, and, so far as possible, of the part it has still to play in evolution. I am aware that this ambition would yesterday have brought, and may still bring, a smile of derision to the face of the reader. But our evolutionary scheme showed us at a glance a vital force which seemed to suffice for the physical framework of life and, thus encouraged, I propose further to analyse that scheme, and to put together all the manifestations of the psyche we can find in it. Our business is to analyse these manifestations in the light of our own knowledge of the psyche in us.

Practically, all that we have hitherto known of the nature of the psyche itself has been from within, but now it is possible to find out the physical conditions that are associated with definite mental conditions, and then, with the aid of our rhythmical sequence, to postulate those same psychical conditions, to some degree at any rate, for the parallel physical conditions of earlier periods. It is obvious that, if we can do this—if we can trace the psyche running through the rhythmical series, we shall for the first time see it also, as it were, in bird's eye view, from without.

Given, then, that the psyche is something real—so real, in fact, that not a few of our profoundest thinkers have regarded the three-dimensional environment as unreal in comparison—our next task is to try to separate the physical and the psychical from one another as two distinct groups of phenomena.

One view of this important question that has pre-

veiled even among biologists of eminence is so instructive and significant that it deserves notice. Man's physical frame, it is asserted, is the product of physical evolution, but when human societies appeared, he became endowed with a soul, breathed into him in some mysterious manner. This suggestion was only possible to those who held the older view of evolution, at a time when the details of the evolutionary process were hazy and its stream could only be seen in broken fragments coming along towards us through the ages, here a little, and there a little, without visible continuity. There was then no reason why biologists should not find it possible to imagine some interruption of continuity, such as the sudden "inspiration" of a "human soul," now quite impossible for us to conceive. In saying this I do not imply that no links are wanting in our more complete sequence, but the missing links in our case leave no uncertain gap into which anything quite so unexpected as a human soul might slip. The proper filling for every gap is already known in general outline, for it must fit into that part of the periodic formula to which it belongs. But, under the old view, such a claim could be definitely made, in order to account for the mind of Man, with all its mysterious artistic and scientific perceptions, dwelling in a purely physical body. It was granted that Man, as a material animal, had been evolved from earlier, simpler animals along the ordinary physical lines of evolution, whatever they were, but how is it possible, it was asked, to evolve his marvellous psychic forces without some quite new and distinct addition to those forces; an addition which may be called spiritual?

This view is referred to here by way of showing how definitely Man has emphasised his conviction that

mind and matter are absolutely distinct—that the body evolved slowly within and out of the three-dimensional environment, while the mind had some other, “spiritual” origin. In itself this view is untenable. It has been again and again refuted on the ground that we see the beginnings of the psyche in animals lower than Man and that, in view of these earlier appearances, it is arbitrary to try to introduce the psyche as from outside of the sphere of evolution. Both history and individual growth show us that it certainly does evolve along with organic growth, and is eminently capable of further evolution. To us now, with our new evolutionary hypothesis, the apparently sudden “appearance” of a soul is explicable without any interruption of continuity. Each period runs its course, no factor intervenes except such as rise out of the complexities built up by the series itself. The sudden outburst of the “mind of Man” in the fifth period was inevitable if our rhythmic series was to be continued. The psyche was, we may say, simply brought to the surface and “externalised” for the purpose of building up social aggregates.

The doctrine of sudden inspiration from some spiritual source, which has here been mentioned as untenable, was never universally accepted, for it was clearly seen to be philosophically incompatible with evolution. As soon as the conception of organic evolution was established, it necessarily involved the assumption that each organism, with *all* its powers, must have been produced by a chain of comparatively simple, intelligible causes, in which there was no room for chance alterations or intrusions. Our physical frames were recognised, not only in texture but also in function, to be merely concrete and condensed embodiments of the natural

processes by which they had slowly come to be—of all the processes, at least, except those which have been secondarily eliminated and passed over as no longer necessary. These processes are not now spread out through the ages, but occur together, superimposed, as it were, before our eyes in one single visible and analysable mechanism of surpassing intricacy.

This strictly philosophical view is here adopted as the only possible starting point for research. But there is one obvious danger in it, that of losing sight of the profound distinction between mind and body. To regard them both as the results of one great evolutionary process would naturally tend to confuse them once more with one another, and we actually find evolutionary physiologists failing to appreciate the distinctive characteristics of the psyche; some are as confident of being able to translate every physiological process of body *and mind* into chemistry and physics as the anatomist has been of analysing every tissue into cells. It was even hoped that we should be able to show that the brain secretes thought as a gland produces its proper discharge. All the processes of life, indeed, were to be analysed and weighed and measured and reduced to physico-chemical formulæ. This enthusiasm was naturally doomed to disappointment.

But a far more subtle confusion of the spheres of mind and matter still exists, and gives rise to that controversy as to the existence of a “vital” or psychico-psychical force which was mentioned at the beginning of this chapter as still raging. The vitalists argue that, if the psyche has evolved with the physical frame, it is natural to assume that its mysterious powers of intelligence might be utilised to explain all those vital

phenomena which now baffle our ordinary physical conceptions. Life problems which seem imperatively to demand a guiding "intelligence" for their solution are numerous. The assumption of a new vital force, both physical and psychical, was therefore, I admit, very natural; something seemed needed, differing equally from ordinary physical forces and ordinary psychical forces, the two being hypothetically united into one compound force. Now, it is obvious that this hypothesis is like a knot drawn tight in the tangled skein we were hoping to unravel, so far, at least, as to try to obtain a connected series of psychical phenomena as distinct as possible from the physical. To my mind, it seems necessary, for any further understanding of either of them, to keep the two classes of phenomena distinct, those which are undoubtedly physical, on the one hand, strictly apart from those which are equally clearly psychical, on the other. By so doing, we shall obtain, as it were, two more or less fragmentary inscriptions written across the face of life, one psychical, the other physical, like two strange and mysterious languages, both having exactly the same meaning. The discovery of the physical force running through the rhythm in which apparently no psyche is needed, encourages me to try to keep the two separate, though, in time, it may be possible to find the clue to the translation of the one into the other. It is only by endless comparisons of the one with the other that we can ever hope to make any way in unravelling the real underlying unity which we are justified, by philosophical necessity, in assuming.

Such a comparison of a series of psychic phenomena with its associated series of physical phenomena I shall presently attempt, but I must first try to

dissolve this purely hypothetical knot, the "vital" force.

The view so far arrived at is this: I would deprecate the assumption that the psyché has mixed, in any way, as an integral factor in the machinery of the building processes of the forms of life, or in their daily workings as intricate mechanisms. And yet I believe it has been able to exert an influence on the working, in either delaying or hastening it. I make the first statement with the greater confidence, because our evolutionary theory has already revealed a physical force apparently sufficient for the explanation of the physical phenomena of life; and I make the second statement supported by the fact that the nerves are the essential instruments of the psyche in all complex physiological processes; their business is to convey the stimuli, and the extent of free play which they allow the psyche seems to be either to diminish or heighten the stimulus. Except in these ways, the psyche does not normally interfere with the physical processes of life. That no physical explanation can be found for a particular physiological process, I prefer to regard as due to our ignorance of molecular physics in general and of the particular molecular problems involved in the special case.

I would repeat, then, that, while it is quite impossible, with our scanty knowledge both of the molecular physics of the ultimate life processes and of the psyche which in some way accompanies those processes, to say that intelligent guidance is not and *cannot* be given by the latter to the former, I nevertheless demand clear evidence for any such case, and feel compelled, from what our evolutionary scheme seems to tell us, to adopt a strictly negative attitude until such evidence is

produced. The fact that, as knowledge advances, the need for any such interference steadily diminishes confirms me in this attitude. I would here recall two cases in which our evolutionary scheme has already helped us to dispel an apparent mystery. Nothing could be more mysterious, for instance, than that a pile of apparently discrete cells should begin to grow out into one another, as if guided by some intelligent foresight of what each cell was required to do in order to form a mechanical whole. Once, however, realise that these cells are all, in reality, united by a subtle filamentous network which runs as a continuum through the whole pile, and there ceases to be any special mystery in the fact that some of the filaments become nerves, some muscles, and others become coated with skeletal matters of different kinds and consistencies. Here was a problem which clamoured for some associated intelligence, but its solution was found in the natural reactions of a living, rather diffuse whole, to environmental stimuli. That such and such reactions have such and such physiological and morphological effects may still be quite inexplicable, but that is simply because we know too little of the molecular physics involved. No one would think of demanding a special vital force for their explanation.

The second problem which this new view as to the fine structure of protoplasm seems to help us to understand is that relating to heredity. It provides us at least with some kind of escape from the present atmosphere of mystery in which it is surrounded. Nothing has been more mysterious, for example, than the development of an egg. An egg appears to consist of simple protoplasm and, so far as our powers of observation extend, one egg is, in essentials, very much like

another. And yet, when the eggs start developing, each produces unerringly the form, however complicated, of its parent, even down to the surface markings. This was thought to be specially mysterious because, although the egg is in the parental body, it appears to have no organic connection with it. It has been regarded as a separate cell, and the growth of the parent with which it is said to have no organic connection is therefore unable to influence it in any way conceivable to physics. Here are mysteries which our continuous filamentous system once more helps us to dissipate. In the first place, the egg was and remains but one of the nuclear centres in the fundamental network of the parent, and is at the same time possessed of its own subtle network which supplies it with lines of growth upon a definite plan. In the second, the network of every egg, until it becomes actually detached from the parent, is in direct continuity with the underlying network of the parental body.¹ Even though it may still be difficult to understand how the individual growth of the parent body is able to record itself upon the constitution of the stationary egg, which was simply a part of that body early held back from the growth that affected the rest of the organism, we are able to assume that the egg thus held back might itself conceivably store up the growth stimuli, holding them back, as it were, until its own growth becomes possible. Then that growth will be of the kind which these stored up stimuli demand and which, when released, they have to guide.

We are still further confirmed in denying that the psyche has ever played a part as mechanician in the building up of the forms of life and, on the other hand,

¹ See Pt. I, p. 259.

encouraged in referring the subtler processes of life to ordinary physics, by the explanation our theory gives of the whole of material evolution, that it is due to the action of one primary force, the alternation of aggregation and segregation taking place in complex chemical molecules, and the interaction of this force and its results with the forces of the environments which it meets and even creates. So long as we keep this in view, the demand for a new and special vital force to help out the physical seems out of place. The subtleties of the molecular forces are only beginning to be studied. For all we know, a regularity of movement like that of the celestial bodies may be maintained among the constituents of the smallest molecule. Not only so, but every disturbance of these movements may be repeated and registered through all time, until once again modified. These conceptions may be strained, but it must be admitted that they are possible, especially when we know that the ultimate effects of what we have to explain, being chemical and physical, have to be traced back to the interactions of the chemical elements concerned.

Such conceptions are helpful when we remember that the most complicated and apparently mysterious life-process has had small beginnings and has taken ages, as it were, to learn how to act its part. Processes which seem to us absolutely inexplicable without some intelligence to guide them through their intricate mazes of action and reaction may be very condensed repetitions of great numbers of infinitesimal molecular reactions which took ages to acquire. What happens now may appear specially complicated owing to the necessity of the molecules to repeat and register disturbances and modifications which took place long

ago, and are now wholly unintelligible. This may sound rather like special pleading. But are we not justified in this assumption by the fact that embryos are known to 'develop organs or the traces of organs which have long vanished from the adult,¹ and are thus condemned to build up apparently only to pull down again? This fact looks more like automatism than intelligently guided growth.

I therefore feel confirmed in my view that the assumption of a special "vital force" is a knot gratuitously tied in the tangled skein of physical and psychical phenomena. We find the two associated, it is true, most intimately, but, if we wish to discover what the nature of that association is, we are only blocking the way of research if we assume it to consist in a psychico-psychical "vital force" whose chief action is confined to bringing about a few intricate molecular physiological processes in the building up of life. The physical forces are great and imposing enough as we know them, apparently working without help of a psyche, while the psyche builds up its vast creations in the world of thought and sentiment apparently without the need of direct help from any of the physical forces. We know, of course, that the two are not so absolutely distinct; the evidence shows them to be, in some way, mutually interdependent. What the nature of that interrelationship is has to be worked out in detail and the assumption of a vital force is, to my mind, inadequate and useless; it seems, indeed, to be a hindrance to any real advance.

I would conclude this discussion, therefore, with the suggestion that the psyche does not take part in the

¹ *E.g.*, the appearance in the embryo whale of teeth which are resorbed before birth.

actual machinery as any primary essential part of the mechanism but, as the machinery becomes complicated, it plays an important part in simply heightening or damping down the stimulus.

CHAPTER XXIV

ATTEMPT TO ANALYSE THE PSYCHIC ELEMENT IN LIFE

HAVING cleared our minds of any hypothetical methods of union between the physical and the psychical, assumed in the interests of either scientific or religious thought, we are free to appeal directly to life as illuminated by our evolutionary theory and to endeavor to extract from it, by the disentanglement of the classes of phenomena, some idea of the laws of their association.

What we call Life to-day is obviously made up of some intricate association of the physical and the psychical elements. We are justified in assuming that, starting from some primitive condition, the association, as we now find it, came about gradually in the course of evolution. Our evolutionary theory seems to show life in its earliest stages as having emerged, by definite and rigid periods, out of the inorganic without, however, ever leaving it and now, in the fifth of our traceable periods, we see it rising into the psychical but without ever leaving the physical. This is in accordance with what has already been suggested as the meaning of evolution, that it is a progressive advance and exploration of the environment, going ever deeper and deeper into its subtleties. Our immediate task in this chapter is to compare the phenomena of life, series with series, the admittedly physical series with the

admittedly psychical series (in so far as they lend themselves to comparison), to see if we can obtain even the remotest clue to the nature of their association.

We do not know what either the physical or the psychical is in essence, but we know for a fact that they come into association in animal life. They may, for all we know, touch each other at all points in the whole universe. We, however, only have certain knowledge that they touch one another in animal life and are apparently in much "closer contact" in the life of Man, as the unit of a social organism, than in any of the forms lower down in the evolutionary scale.

It may help us if, at this stage of our enquiry, we try to obtain some clear idea of what we mean by life.

So much has been written about life that it would seem hopeless now to find anything new to say about it, yet I believe that it is possible to improve upon the best approximate definition that has hitherto been given of it. Herbert Spencer has defined it as "the continuous adjustment of internal relations to external relations." This, like the same philosopher's definition of evolution (p. 308), is a brilliant abstraction, the general truth of which every one must recognise. It was not claimed as anything more than an "approximate" definition for, since we do not know what either matter or mind is, it is obviously impossible to give a complete definition of that mysterious association of the two called life. Quite apart from this admitted limitation, however, the terms of this definition do not seem altogether satisfactory in the light of our new evolutionary theory.

In the first place, no attempt is made to discriminate between any of the kinds of relations referred to as "internal" and "external." Life, in its purely physical aspect is well described as the adjustment of internal

to external relations, for the organism, as a physical mechanism, attacks the physical environment and either succeeds or is repulsed. But, associated with these physical attacks and repulsions, there is some psychic accompaniment which we call "feelings." Probably Herbert Spencer included these in his "internal relations," but the terms of his definition might be completely satisfied without them and yet there would then be no life. The "adjustment of internal relations to external relations" is not sufficient for a definition of life, for these psychic stirrings are not necessarily part of the process of adjustment, unless—and this is a question of the first importance which will be dealt with later—unless there are also external psychical relations to which the internal psychical stirrings are adjusted just as the internal physical relations are adjusted to external physical relations.

My second criticism is that the expression "life is a continuous adjustment," though true, is quite too tame to suit the facts. The definition was perhaps strong enough so long as evolution was regarded as one continuous and uninterrupted sequence of natural generations advancing slowly and solely by the appearance and selection of chance variations in adaptation to environmental variations, but is quite inadequate to cover the periodic outbursts of life which started the successive periods. Indeed, as soon as the ordinary doctrine of descent is illuminated by the conception of the vital force as the cause of all growth, whether in colony-formation or in the building up of individual organisms as complex machines, each to be dashed against its special environment, some strengthening of Spencer's word "adjustment" seems to be demanded.

The first criticism just expressed—that not all inter-

nal relations are necessarily included in the definition—might be met by altering it thus: “Life is the continuous adjustment of internal relations, physical and psychical, to external relations, physical and psychical.” To meet the second as well—*i.e.*, to include the conception that the essential characteristic of life is its continual and progressive advance,¹ the life force continually driving organisms on to storm and master ever new and larger environments, I would suggest a further alteration as follows: “*Life is the continuous, progressively more extensive and more complex adjustment of internal relations, both physical and psychical, to progressively more extensive and more complex external relations, both physical and psychical.*”

The definition, in this form, is as complete as it seems at present possible to make it. We see organic life, with all its physical and mental qualities, advancing in the face of an environment which is both physical and psychical.

We have next to try to discover how the physical and the psychical are related *within* the organism. On this problem, hitherto apparently insoluble, we now have some chance of obtaining further light, for not only do we find our bodies and minds closely interwoven, but we can see them coming up the evolutionary ascent together and undergoing the earlier processes of that interweaving. By studying these processes closely, we may hope to advance another step.

One of the most obvious parallels between the evolution of the physical and the evolution of the psychical

¹ There is a very real sense in which equilibrium is death, for by it an organism becomes merely a well-adjusted automatic machine of fixed pattern, while the activities of the psyche, with no new stimuli to respond to, would be slowed down to quiescence.

in organic life is nevertheless one of the most fundamental and illuminating. Physical evolution seems to be due to a driving force (*a*) which dashes each organism against some environment. Here it meets with elements of attraction (*b*), with others that merely awaken curiosity (*c*), and others again that are repellent in all degrees of repulsiveness (*d*). Now, no one can help noticing that, in the psychical sphere, we have a parallel evolutionary series. We have a will (α) driving us forward; let us say that this is the psychic equivalent of the prime physical force (*a*). We have pleasures (β), in all degrees of intensity according to the attractiveness of the objects (*b*). We feel curiosity (γ) with regard to objects that neither attract nor repel (*c*), and, lastly, we have pain or disgust (δ) at objects that repel us (*d*). This parallel has only to be stated to be acknowledged as true: *a, b, c, d*, in the physical sphere, find a striking parallel in $\alpha, \beta, \gamma, \delta$, in the psychical. It may be difficult to see at a glance that the will is the psychic equivalent of the physical force of doubling division, but no demonstration is needed to satisfy us that pleasure and pain are the psychic equivalents of the attraction towards attractive objects in the environment and of the repulsion from repulsive objects. This is a matter of daily experience.

This parallel, lying on the face of our evolutionary theory, seems to place the existence of some kind of parallelism beyond all doubt and to lead us to hope that, by extending the parallel and examining it very closely, we may obtain some dim idea of the inter-relationship we are trying to unravel.

Now, in order to obtain any series of psychic phenomena which can be parallel with any series of physical phenomena, we must first of all find some kind of

psychic experience which has an element of continuity in it. This is not the case with our joys or sorrows, which are proverbially intermittent, following one another without order, and having nothing regular about them except their waywardness. It is otherwise, however, with our growth in *knowledge*. There is always an environment, and, except during the intervals of sleep, we are always being driven against it. Stray spots of that environment give us pleasure, others give us pain, but the mass of it acts solely upon our curiosity,¹ and thus builds up our knowledge. Since, however, pleasures and pains are but special kinds of psychic experience, we may include them in that larger score of experiences which together make up our knowledge.

In this never-ending sequence of experiences, we find a continuous physical series and a continuous psychical series. The physical frame seeks to adjust itself to the subtleties of the physical environment, while the psyche, with its feelings, as it were, tastes them all. Among these subtleties we have to include such psychic traces as are specially pronounced within a social organism which makes both a physical and psychical environment for each one of its units, and all traces of an external psyche which can be found intermingled with the physical environment. If this can be worked out in detail, if we can take our physical evolutionary framework and trace the growth of the

¹ It is specially pertinent to our present enquiry, the evolution of knowledge, to ask whether pleasures and pains are more elementary phenomena of the psyche than curiosity. What is curiosity but the psychic equivalent of that attitude of enquiry and hesitation as to the exact direction the organism has to pursue in face of a complex environment made up of bitters and sweets lurking everywhere in a multitude of disguises?

psyche alongside of it, step by step, and upon it as if it were a vine growing out along a trellis, we shall have a startling parallel indeed.

In order to make this perfectly clear, we have to go back to the method of the first appearances of the psyche in the building up of the human aggregate. Psychic phenomena are, we know, associated with physical stimulation of nerves. In the building up and welding together of all earlier colonies, any stimulus at the surface of the colony travels through unit after unit along continuous nerve fibres and thus affects the whole organic colony which tries to respond as a whole. The response would at first, of course, be wild and chaotic, like the blind charge of a herd of cattle if all the animals were chained together but, little by little, the colony would become centralised for ordered responses; the herd would give place to a well-ordered army with a controlling centre, and the colony would become integrated into a new organism on a scale visibly higher than was possible to any of its component units had they remained single. This centralisation was the only alternative to speedy dissolution or destruction. How far the nerve stimuli, as they rushed through such an organism and led to its gradual integration,—how far, as they passed through the units, they woke up any psychic disturbances in those units, we do not know. We may safely assert, however, that some were stimuli of attraction and would awaken some thrill of pleasure, others stimuli of repulsion awakening some thrill of pain, and these pure sensations belong to the psychic sphere. Some play of the psyche can thus be traced hovering over the nerve stimuli even in the evolution of the simple colonies as they lapse from the homogeneous to the heterogeneous.

It is to essentially the same process in the fifth period that we can trace the special outburst of the psyche, as the natural result of the new conditions. We have to remember that, in the case of human societies, there are no continuous nerve fibres to send the stimuli automatically through the aggregate, but each individual unit has, within itself, an immense store of nerve energy. Only rarely do the stimuli arrive as waves of terror or other emotion, sweeping the unit along; they mostly come in stray and broken fragments awakening the nerve energies of the units into nerve storms which struggle to express themselves in fresh messages in all directions. Every unit of a human social aggregate must therefore be in a more or less perpetual nerve agitation of all degrees of violence. If psychic phenomena are, as a rule, associated with physical nerve agitations, each unit must, from the beginning of human colony formation, have found itself the centre of a continuous whirl of psychic experience.

If this analysis is correct, let us note that we have succeeded, on our way to the establishment of a continuous parallel between physical evolution and the evolution of knowledge, in carrying the general and obvious parallel with which we began between psychic pleasure and physical attraction and so on, inward, into the very heart of the organism or, so to speak, down to its fundamental physiology. We have thus traced the parallelism, first as a general truth, secondly, as extending to the very foundation of life, and now, thirdly, we have to show it as having been continuous from the beginning. This we can do if we can show that the evolution of knowledge has progressed hand in hand with the evolution of the physical frame.

So as to make any such outline sketch of the evolu-

tion of that element of the psyche we call knowledge, we must go back to earlier, simpler conditions. We must start with the elementary facts that psychic affections are invariably associated with agitations of nerve tissue and that, of these many different kinds of nerve agitation, one accompanies the psychic sensation of curiosity. Now, we know that there must have been, and still is, a simpler condition of every kind of organic tissue. The nerves, for instance, are secondary specialisations of the undifferentiated filaments of the fundamental linin network. But we may, for the present, ignore this early stage and begin with the minutest organism which had its network of filaments projecting all over the surface as sensitive points and functioning as nerves, *i.e.*, an organism possessing the essential characteristics of the successful units of structure that have built up organic life. Every contact of this organism with its environment must have meant some stimulus to the nerve endings, and these must also have meant varying psychological disturbances.

But every physical nerve stimulus is subject to laws which have to be carefully noted, and we have to seek for the parallel laws governing the psychic disturbances that accompany the nerve agitation. Out of these earliest beginnings, governed by these elementary laws, the later complications have been built.

We may note, then, several characteristic phenomena connected with all sensation. However sudden the impact may be, all sensation lingers for awhile and only gradually fades away, the length of time that the sensation lasts having some relation to the violence of the impact.¹ The importance of this will be evident

¹ The lingering of a sensation of light on the retina may serve as an illustration. That it lingers *as light* after the actual light stimulus has

when we come to consider the growth and continuity of knowledge.

Another characteristic phenomenon is that nerves tire and that the same stimulus, after a time, loses its power of causing excitation and consequently of awakening the psyche, so that an interval is necessary to allow the nerve to rest before the sensation can again be aroused. Hence the beginnings of stimulation are the moments of greatest psychic excitation and the release from stimulation is a distinct kind of feeling,—a relief or a loss. The reader will notice a close parallel here between the physical agitation of the nerve and the psychic sensations; they rise and fall together.

By way of illustration, let us take a small organism thrust by the force of division into an environment which would necessarily be somewhat uniform, say, a microbe in some nutritive semi-fluid mass. There would not be any great amount of nerve stimulus, for the permanent stimulus of the contact surface would lose its power of exciting the nerves. The changes in such an environment would be comparatively slow and would hardly be able to linger long enough to awaken any continuity of sensation. The several sensations would be few and far between, and not all would be coherent enough to give rise to a perception. We see here, more clearly than ever, the danger to the psyche of a stationary environment and the great part played in its development by incessant rapid locomotion. The stimuli, under such circumstances, are not only rapidly but continuously changed,—changed, that is, in continuous series, giving wider and profounder

been withdrawn is not due to any characteristic of the nerves but mainly to the gradual retraction and quiescence of the pigment between the rods.

perceptions into the nature of the environment than are possible to a stationary organism whose changes are only those that come from the immediate environment, *i.e.*, from chance variations in its contact surface. We see also more plainly the disadvantage of works of defence. Every armour plate, large or small, is of the nature of a blind spot, and so far a hindrance to knowledge.

And here we may note another parallel, *viz.*, that the same process that raised organic life in size and complexity so as to attack and overcome larger and more complex environments, served also for the advance of the associated psyche. Colony-formation had the effect of vastly increasing the contact surfaces of organism and environment, and consequently of multiplying the number of sensitive nerves projecting from the surface and of allowing many to run together into coherent series, the result being distinct perceptions. Sensations arising from environmental impacts would now follow fast and frequently, and their lingerings would cause them to overlap, to run into the definite sequences necessary to perception, to intermingle and neutralise one another. At first, indeed, great confusion would result, for each colony would consist of a number of units, which would not only be nervously disturbed by the receipt, along the connecting nerves, of many and conflicting stimuli from the surface, but would also be greatly hampered by the fact that, unless they were placed at the surface, they would be unable to contribute any direct effective response; they could respond only through fellow-units which were perhaps feeling quite other stimuli, or were absorbed solely in their own internal metabolic and physiological necessities. We can well believe that the life of an incipient

colony was a veritable tower of Babel. It need hardly be pointed out, therefore, that the centralisation of the lines of stimuli which was indispensable for morphological and physiological integration was also necessary for the co-ordination and development of knowledge. Only when the nervous system was centralised could the stimuli at the surface, which had till then been merely confusing, or we might say, in a real sense, "maddening," give coherent messages as to the nature of the environment. In a centralised system, the stimuli with their lingerings would run together into sequences both in time and space and, instead of isolated sensations, definite perceptions as to the character of the environment would be possible, and the different attractions, curiosities, and repulsions distributed round the organism would become distinguishable. Knowledge thus grew hand in hand with the development of the *nervous system as the organ of the psyche*.

So far, then, there are certainly a great number of psychic phenomena taking a very fundamental part in the formation of our brain activities which can be shown to be, in some way, "reflections" of purely physical phenomena. The will, pleasures, curiosities, pains, and now even the whole process of the accumulation of knowledge, can all be shown to be the psychic counterparts of physical processes.

The further we advance in these parallels between the physical and psychical phenomena which make up the life of Man, the closer do they seem to become, and they make us bold. They suggest that all mental phenomena must have their physical counterparts. Following this suggestion, I turn, though with some hesitation, to the mysterious subject of the memory. There is, of course, nothing more intrinsically mysteri-

ous in memory than in any other psychic phenomenon. Given the psychic equivalent of any nerve stimulus, we have already seen that, up to certain limits, it is strong if the shock is violent, and weak if the impact is slight, and herein, as already pointed out, we again have a parallel in the psychic sphere to the physically strong and the physically weak nerve stimuli. This strength or weakness of stimuli naturally suggests a still further parallel as perhaps existing between physical and psychical "scars." Inner marks might easily be in some way left upon the system of ultimate nerve filaments by the strength of a stimulus, and these physical scars may find a parallel in memories left by the vividness of the psychic sensations which resulted. We know, as a fact, that memory may be greatly impaired, or even destroyed, by injuries to the brain, *i.e.*, we may imagine, to areas in which these memory "scars" are plentiful. Such scars would vary in depth and durability. A certain proportion of them, namely those associated most intimately with the environment and with its most frequent impacts, would be constantly deepened by repetition of the stimulus, until they become permanent features of the co-ordinating centre, and eventually inherited. All structural changes gradually brought about in adaptation to environments would thus be closely followed by the psyche, and would be recorded in memory, and might even become inherited memory. We call such cases instinct, or inherited habits of thought. But quite apart from those instincts which are useful, it is possible that traces of others, such as inherited terrors and joys, accompanying certain experiences or associated with certain sights and sounds, may also be handed on from generation to generation and

may supply the basis for many of our subtler artistic impulses.

Problematical as these hypothetical memory "scars" may be, we can hardly doubt, in the face of so close a parallel as we have succeeded in indicating between the psychic and the physical in the evolution of Man (as if they were, indeed, reflections of one another in two different media), that such associated psychic phenomena as memory and forgetfulness have their physical counterparts, although the exact nature of the parallel may baffle research.

One other parallelism already hinted at deserves to be emphasised.

One of the most fascinating chapters in Professor James's *Principles of Psychology* is that entitled "The Stream of Thought." Through all our waking hours thoughts flow automatically and without ceasing through our minds, and intermittently also when we are asleep. The explanation of this seems to be that we are at all times in the presence of an environment and can by no possibility escape from it, except only during the soundest sleep. We are being forever driven by the life-force either to master it or to perish before it. We have it perpetually before our mind's eye, and have to scan it whether we will or not. If, in doing so, we are always eager for some new light on the enigma of life, we are either religious or scientific enthusiasts according as we look for more light from the psychical or the physical elements of the environment, and the two classes of temperament shade off into one another. Such persons are mostly energetic, those in whom the life-force has free play. The majority, having less force, are chiefly eager to discover attractive spots out of which to get a moment's happiness, and to avoid or escape

those which threaten unpleasantness or are unpleasant. These latter unpleasant elements of the environment are obviously more educational, because we give ourselves up to happiness with a fatuous acquiescence, whereas we have to put out our energies, both physical and mental, to escape the hardships of adversity.

This incessant "stream of thought," so eloquently described by Professor James, seems to sum up and put the cap on the series of parallels that we have been drawing between the chief characteristics of mental and physical phenomena. The mind is as active as the ever wakeful body. It is always, as it were, scanning the environment, physical and psychical. Whenever the three-dimensional objects are not claiming its attention, it is "brooding over" some mental or material matter relating to distant objects or persons. These mental processes, indeed, may become so all-engrossing that the physical environment, however beautiful in color or form, may be of no account. Our new view enables us to see this "stream of thought" passing perpetually through our minds, not only from within, but from without, as the sequence of sensations caused by our daily or hourly progress through a medium consisting of both physical and psychical elements which are associated with one another and seem, at times, to pass into one another, but yet are distinct. In this way the "stream of thought" practically sums up our series of parallel phenomena, for it is the psychic counterpart of our perpetual contact with the environment.

Now, what can all these parallels tell us as to the relationship of the physical to the psychical? How are we to picture it to ourselves?

First of all we have to dismiss the notion that there is anything more specially divine and "supernatural"¹ in the mind than there is in the body. We may gather this from the fact that our thoughts delude us just as our sight may deceive us. If our vision is defective, in either the physical or the psychical sphere, we dash ourselves against unseen objects (untruths) in the environment. That the mind is a natural evolutionary product is also shown by the fact that psychic phenomena are associated in us with some stimulation of the nervous system, of that system which has been one of the natural organic phenomena from the first. Further, we now seem to be finding out, through telepathic phenomena, that disturbances are able to pass from the nerves of one unit to those of another through the intervening medium, and, by their transmission through space, suggest that they need not, in reality, differ fundamentally from ordinary physical forces. This suggestion must not, however, be carried too far, for, when we remember the nature of the stimuli that pass from unit to unit, either directly (telepathically) or indirectly (by signs or language), we recognise that, whatever physical elements may be associated with them, such as physical agitations in the nerves, there are psychic elements wholly different in kind from the physical elements, known as sorrow, joy, love, hatred, bewilderment, pain or humor, enthusiasm, ecstasy, frenzy, and such like. These are all quite distinct from the physical attractions and repulsions of molecules, or any of the phenomena of our three-dimensional environment, and yet all are apparently

¹ We use the term "supernatural" in the ordinary sense, *i.e.*, outside, "above any recognised law." For every phenomenon that is proved to be governed by law becomes thereby "natural."

equally real. These, and a hundred other mental phenomena, constitute, in a way impossible to define, a new character, quality, element—or shall we at once boldly borrow a term from mathematics and call it a new “dimension”¹ of our environment, hitherto three-dimensional?

These various mental conditions lead us to believe that, at any moment, while being driven through this three-dimensional environment, we may also be plunged into a psychic condition which hangs like an atmosphere over our particular physical surroundings. We may suddenly find ourselves in a joyous or a painful atmosphere which is quite as real as any of the impressions made on us by our more ordinary physical senses. We have hitherto regarded the physical alone as real. Is that not simply because we have so long been familiar with the rocks and trees, fire and water, etc., which share the physical environment with us as physical organisms? Now we are beginning to realise that, all the while, there has been a subtler environment interwoven with these familiar physical facts. A new element of the environment begins to dawn on us and becomes specially prominent when other living things become organically related to us as mutually dependent units of a social organism. We all form part of the three-dimensional environment, but we have

¹This term will be used in the following discussion, and the psyche will be referred to as a fourth dimension, simply because mathematical terminology supplies me with the most convenient figure of speech to convey what I wish to say. I myself have never been able to conceive of any fourth dimension in mathematics; others, I believe, have done so. I do not mean what they mean, but merely borrow the expression for what I myself mean, viz., that every physical fact that goes to make up our lives has some kind of “reflection” of itself, which cannot be regarded as existing in any of the known dimensions of mathematics.

become aware that its attractions and repulsions are more than physical.

Have we not facts enough here to allow us to advance a little further, admittedly, of course, on very thin ice, and still clinging, in these nebulous regions, to our mathematical figure, and say that just as the three dimensions have names (length, breadth, and depth), so this new "dimension" may have some name which must signify both knowing and being known?—the familiar word "psyche" would do if this meaning is passed on to it.

There is nothing new, in evolutionary conception, in the psyche advancing in the knowledge of itself, for the organic framework is simply the advance of a physical organism through the physical environment. But while we can hardly speak of a physical organism knowing its physical environment, knowing seems to be the special characteristic of the psyche, so that we may provisionally speak of the psyche in us as knowing and gradually learning to know, and of the psyche outside us as being continually known.¹ We are just beginning to wake up to this external psyche as a definite element in the environment. Though we may have been scientific thinkers in other lines, we have never yet been able to be other than religious dreamers in the presence of the psychical, dreamers who have long realised that there must be something there, some other side of life which has been called "spiritual." This something,

¹The obvious suggestion that the external psyche is also "knowing" opens up a question too great for us here. However this may be, we can gather from the fact that the interaction of the physical without and the psychical within is paralleled by the interaction of the physical organism with its psychical environment, that the external psyche, like the external environment, is governed by laws and forces as subtle and as intricate as any which still baffle the science of physics.

offering strange and various aspects, the exploration of which is essential to the further growth of our minds, seems to begin at last to take shape as a fact of science.

One step further I am led, whether my readers, who now have before them my statement of the facts for what they are worth, can follow me or not. From the first, the nervous system projected all over the organism so as to feel the environment; it was essentially a sensory organism. Each unit of each period was found to be characterised by the same exquisite sensitiveness, at first almost entirely tactile, olfactory, or gustatory, the difference being merely that the tactile organs are sensitive to mechanical, the olfactory or gustatory to chemical impacts. Later, auditory organs and visual organs were added, so as to increase the sensitiveness of the organism to the environment. All these, added to the tips of the nervous system, increased its functional perceptions as essentially a great sensory organ. From the first, therefore, the nervous system, with all its sense organs taken together, has been essentially a sensory organ. We have hitherto recognised it only as so many sensory organs joined together by an elaborate centre for the purpose of co-ordinating the messages received, for only by such co-ordinations were these organs of any use in the guidance of the organism through the environment. A poor aim indeed if that were all! But now we realise that, with every stimulus travelling inwards from an external impact, there has been a psychic disturbance, associated in some way with the molecular disturbance in the substance of the nerve, and though we have no conception of the nature of the psychic disturbances caused by these stimuli, we need not be surprised if the great nerve centre which was, so to speak, their theatre, and which, with every

advance in evolution, became larger and larger, finally developed into a special organ of the psyche. With a sensory organ for the appreciation of psychic phenomena thus added, we have a vast complex sensory apparatus for the exploration of the whole environment, physical and psychical, consisting of peripheral organs for the mere surfaces of the three-dimensional elements and a special central organ for the more subtle mental perceptions.

CHAPTER XXV

THE PSYCHE IN US AS A FACULTY OF PERCEPTION

THE last chapter ended with a suggestion that what we usually term the "five senses" were the senses earliest developed and specially adapted to guide us in relation to the physical element in the environment, while the Psyche, which has long been known as functionally belonging to the nervous system, may be considered as the sense last developed in order to perform the same duty in our relations with the psychical element in the environment. This view gives unity to our conception without, in any way, degrading our view of the human mind.¹

It is clear that if the life of an organism is essentially the exploration of its cosmic setting, then we must have faculties for this evolutionary purpose. So long as the three-dimensional environment was the only one to be explored by the living organism, the five senses were sufficient, and the psychic capacities of the nervous system, so far as we can estimate them, seem to have remained in abeyance. On the formation of social aggregates, however, the probing of the psychical environment came to be essential, and psychic faculties were needed by the human units. The materials for psychic perceptions were supplied by the co-ordinating

¹If any one thinks that this conception degrades Man, he may find consolation in the fact that it exalts the environment.

centre of the nervous system. That this is the special seat of the perceptive faculties is borne out by the fact that, as life became more and more complex, with an ever-increasing number of experiences to record and co-ordinate, the masses of nerve tissue increased in complexity until they reached their highest development in the frontal lobes and brain of Man. The central position of the brain is also not without significance, for, among its functions from the very first must have been that of memory, or the keeping of a record of all the life experiences, whether of the physical or the psychical elements of the environment. It is reasonable to believe that all the records of life received at the centre would in some way also be recorded there, those recently entered still fresh and clear above the confused and fading records of earlier times. It seems, indeed, as if a more elementary psyche must have been busy, co-ordinating the new stimuli with one another and with the old, long before the more developed psyche found external expression in Man and in social life. I say "must have been" because we find the lower forms of life acting upon memory. There could be no evolution of special habits if memory played no part in guiding them, and memory itself seems to imply a psychic function.

Human aggregates, equipped with new powers of perception, have thus to continue the advance of organic life into an increasingly complex environment. If these new powers are, as I believe, perceptive powers, all real progress depends upon and is, in reality, an advance in our powers of accurate perception. This is clear enough in the case of all the great progressive steps taken in science and in the mechanical applications of science which have char-

acterised the last century. They are nothing else than progressive stages of insight into the laws and combinations of the physical three-dimensional environment, leading to a continual advance of knowledge with regard to its intricacies. Man, being driven to advance, does so first of all by experiment; the moment he gets a hint of hitherto unrecognised physical possibilities, he makes experiments, which are of the nature of plumb-lines dropped into the still unknown environment. If these show solid ground, the new knowledge is turned to account. Must not advance into a psychic environment come about in the same way?

In claiming that the human organism can advance into the psychic environment, I am assuming that the character of the environment demands such advance, and we must therefore first look a little more closely into the question of the existence of a psychic environment.

Some kind of psychic environment there must be as soon as human beings form organised societies in which psychic intercommunication becomes essential and gradually develops for the greater efficiency of the social organism. The closer and more organised the society becomes, the more does the life of each unit consist in the adjustment of his psyche to that of his social environment. Here then we have a psychic environment arising within the social organism from the mutual activities and overflowings of the psyches of the individuals constituting the society. Each individual lives in an environment trembling, we might say, with the vibrations started and maintained by the nerve energies of the other units; each member of the society has, as it were, a psychic web

woven round about him and his psyche is stirred by the psychic storms in the minds of others. Of the vast realm of the psychic, the region which lies nearest to us is that of our fellow-men, and it is in this region, that of the psychic relations of man to man, that we seem, as we shall see in a future chapter, first to see new possibilities in the way of experiments which may enable us to advance to new knowledge of the social psyche.

The human mind, however, seems at all times to have intuitively postulated a larger psyche than that discoverable in our fellow-man, as the most important element in the psychic environment. I use the word "intuitively" with a definite meaning. For, if the human mind is a psychic perceptive organ, like the eye, for instance, it sees much more than it understands or can take in. Any glimpse of life shows, if I may say so, far more than we ever see. Man is born, for instance, and comes into life—that is all we see; he dies and goes out of it—that is, again, all we see. But the psyche knows that life came from somewhere and that it goes somewhere, and that "somewhere" haunts the mind. Nothing was seen but the absence of anything where continuity demanded that something should be, but this is, in itself, a negative perception.¹

That we have some evidence more satisfactory than such merely negative perceptions in favor of a psychic element in the environment is, however, I think, shown by the existence of religions among all but the lowest races of mankind. As the psychic perceptions of the units of the social aggregate developed under the influence of social life, some mysterious psychic element

¹A perception neglected by the vast majority in their hurry through life; only thinkers brood over it and puzzle in vain over its significance.

was dimly apprehended by them. That these dim perceptions found very varied expression is just what we should expect. The same diversity occurs with regard to the nature of any mysterious physical object at too great a distance to be seen clearly; speculation runs riot as to its real form and structure. The many and varied religions which all postulate some psychic element in the environment may, I think, fairly be claimed as witnesses to the existence of such an element.

As another form of "dim perception" of this element which may lead to real advance in knowledge, those phenomena which are becoming increasingly familiar under the term "subconscious" must not be overlooked.¹ The conscious mind has been compared, by a great psychologist, to a coral atoll which just emerges above the waves as a narrow ring, and he suggests that it bears somewhat the same relationship to the complete mind as that atoll bears to the whole reef that stretches away beneath the waves as a vast, solid mountainous mass resting on the floor of the ocean. May not this wonderful and inspiring simile be a true account of the facts? It does not seriously differ, in content at least, from what I have suggested, that the mind is a great perceiving organ. Like all organs of vision, it is far from perfect; it has its centre of clearest

¹ I am not alluding here to those subconscious phenomena which are evidently due to lurking memories of the past that still endure as whispered messages, but to those which refer to knowledge of the future, *i.e.*, to environmental factors that have not so far been subjects of consciousness but are appearing, like distant objects, in hazy outline above the horizon and are slowly coming within the area of clear vision. Such phenomena might more aptly be termed "supraconscious," as still above and beyond our immediate reach; they loom ahead of us like mountain ranges that have still to be crossed.

vision, and round this are vast areas of hints and faint impressions as to objects still far off and out of focus.

I would also claim the science of mathematics as a demonstration of the fact that there is a psychic element, one which is probably commensurate with the whole physical environment. Mathematical sequences are purely psychic sequences. They certainly correspond, here and there, with ascertainable physical relationships, such as that "2 and 2 make 4." From such simple numbers, however, mathematicians have built up series of imaginary relationships which are apparently rigidly true in the pure psyche, but whether these express, in any way, relationships which exist in our cosmic setting is a matter not yet ascertainable. This, however, is certainly a legitimate presumption, since an ever-increasing number of such physical relationships of our setting—indeed all that have any element of constancy in them—can be shown to fall naturally and easily into mathematical expression.

I do not pretend to sufficient philosophic ability to enable me to deal adequately with the significance of this correspondence, but, regarding the mind that has traced out these rigid sequences as essentially a perceiving organ, we are compelled to consider these mathematical sequences as perceptions into the environment. Since nothing is perceived but the numerical or spatial relationships themselves, simply as relationships, the mathematical eye would seem to have some power of probing the environment just as if, in the matter of these relationships, the environment were glass. No new concrete facts can be perceived; nothing, that is, except the ever-increasing complexity; the deeper we probe, the more we

are baffled and eventually lost. Does not this ever-increasing complexity mean that the physical intricacy of the environment which we, as living organisms, have still to explore, is equally complex, and that all the relationships of these infinite complexities are capable of psychical, *i.e.*, of purely mathematical expression? Whether we shall ultimately find that any of the purely mathematical relationships that have come out in the more intricate sequences reflect for us psychic relationships we cannot say. If there is any truth in our suggestion that the psychic side of life differs only from the physical as the fourth dimension differs from the familiar three, we should say that this must be so. Indeed, it would necessarily be so if all physical relations have their psychical counterparts. But this is a question that has to be dropped, for it sweeps us at once off our feet.

I am aware that a great universe with a mathematically correct psyche is cold like the cold stars. But is it not merely the great framework of law that baffles us thus? Do we not find intensive specialisations and differentiations of the law gleaming out, with rays of every degree of intense heat, from the psyches of our fellow-units? It is to these that we must turn for our human life. It looks, indeed, as if these intense psychic rays are focussed for us only through the psyches of our fellow-units; by them only are they gathered together into glowing points.¹

Human psychic progress indeed, which involves

¹ In this sense the doctrine of "love" of the great Nazarene was indeed a "revelation." He was able, as it were, to focus on to human life psychic rays gathered from what appears to the ordinary mind to be an environment hard, cruel, merciless, and incapable of responding to the perplexities of the human struggle.

the discovery of fresh traces of these subtler, warmer rays, appealing from the psyche of the universe to the human psyche, seems to be the special function of the artistic sense. It is the artist who, in his literary expressions, in his musical compositions, or with his brush or chisel feels his way to new and harmonious groupings of human relationship, of sound, of color, or of form which speak to us and, for reasons at first difficult to analyse, awaken new emotions in us. From this point of view, what is generally called Art seems to be the gradual gathering in from the vast environment of the subtler and what we may here call the human rays, inasmuch as they are necessary to the life of Man. It is the function of literature not only to discover new emotional perceptions, but to work all these new gleams together into the stock of human knowledge and thus to widen and deepen the whole range of human vision into the things of the psyche. It has been the art of the churches, rather than their intellectual dreams—which latter may, and often do, become frightful nightmares to those who wake up and think rather than feel,—it is their art that has been teaching and leading the generations.

Music affords an apt illustration. We find that musicians have striven after the beauty of sound sequences, following this feeling alone, and it has been discovered that those sequences that give the greatest pleasure, those that are perceived as most perfect by our psyches, are the very ones which, in the numerical relationships of the vibrations of their component sounds, form the most perfect mathematical sequences. May it not be, then, that pleasures, like that of perfect music, await us as we advance farther and deeper into the psychic environment into which evolution is

driving us? Such progress will be almost endless, for, if we may base our argument upon mathematics and regard that argument as not merely academical but as a glimpse into truth, infinite complexities are still ahead of us. If our evolutionary progress does not end with this fifth period, may not the later periods ahead of us carry us, not simply through the cold scaffoldings of the physical laws hinted at by mathematics, but into harmonies more consonant with the cravings of the human heart, harmonies which transcend the highest music we now know even as that transcends the chirrup of the grasshopper?

Before attempting to continue the details of the fifth period of our rhythm along these lines, there are one or two remarks relating to the problem of the integration of the social organism which seem to be necessitated by what we now hold to be the chief function of the psyche, viz., perception.

The prevailing views of human life and its destinies are based upon the assumption that Man has a soul which is housed in his body and that the fate of the body, which, at death, is dissolved into its chemical elements, is of less importance than that of what is called the "immortal" soul. Science rigidly ignores the whole subject as not yet within its scope; no chain of rigid sequences can be found linking this problem on to the foundations laid by science as solidly as they can possibly be laid upon the data that appear to us to be most invariable on the face of mother earth. With regard to matters of psychical speculation, science confines herself to stray criticisms, mostly damaging to any hypothesis dealing with the subject, and this attitude is difficult to change. I would point

out, however, that if the psyche is not a "soul" in the ordinary meaning of the term, but only a more advanced kind of sense organ for the perception of psychic phenomena discoverable in the environment, a considerable change will have to be effected in our general philosophic attitude towards Man and his destiny. Further, our views on some more practical points, such as our judgment of human conduct, must be modified.

The one vital question in connection with human conduct is: "Has Man a free will, or does he act always because he must?" Hitherto, we have had, on the one side, the fabric of the teaching of all the churches as well as the laws of the states, based upon the doctrine of individual responsibility. On the other, the steadily rising conviction that any free will is impossible in a cosmos which is shown, by every new discovery, to be a complex of rigid laws. No final decision could be arrived at because of our imperfect knowledge of the psychic field, and the old view as to Man's being free has been able to hold its own tenaciously. It is hardly fair to say, however, that it was due entirely to our ignorance, because it had at least one strong argument in its favor, a purely subjective one which will be discussed later.

Looking at the matter first objectively from the point of view of our evolutionary rhythm, the case for universal automatism seems to me to be put beyond all doubt. My emendation of Herbert Spencer's definition of life described it as the constant adjustment of progressively more extensive and more complex internal relations, both physical and psychical, with progressively more extensive and more complex external relations, both physical and psychical. But

we are not dashed by the life-force against the environment without recognition of self, experiencing either pleasure or pain from the process. We are only indifferent when we are completely ignorant of what is coming, that is, when our organic psyches have not yet acquired the perception necessary to see the pleasures or the pains which lurk in the particular environment against which we are being thrown. The process is therefore as automatic psychically as it is physically. Physically there is no question that we move in the direction of greatest pleasure or safety according to our perceptions. In these we may be quite mistaken, as when we let ourselves be caught in a trap, but that is when our perceptions fail us. We move then, as always, automatically according to our perceptions. There is no room for any free will, so far as the physical integration of aggregates is concerned, it is purely a matter of the attractive and repellent forces of the environment.

The strongest argument in favor of the existence of free will seems to be found in such actions as deliberate introspection in order to ransack the memory in search of some fading record. We are all familiar with this process. It has the appearance of a deliberate turning away from the environment against which we are being driven, in order to look back. But to see in this an argument for free will is to let ourselves be confused by the complexities which have been increased beyond unravelling. For memory is a factor of our environment, and this action is only a very complicated form of what is simple enough in earlier stages of evolution. Say some simple organism suddenly gets a hint, but without the substance, of some attraction, reminding him that a short time back

he obtained an abundant supply of food. The organism naturally turns back to seek it. There is no free will in the matter, the psyche perceives the record of an attraction and goes back to find it just as automatically as it would have advanced in response to the original hint, had advance been demanded instead of return. The memory is essentially a record of perceptions, and each memory takes its place among those which are being momentarily received from the environment ever fronting us.

If there is no freedom in the purely physical aspect of evolution I cannot see how any can be postulated for the psychic counterparts of the driving physical forces. If the will in general is the "reflection" of the driving force of life it must, like the latter, be purely automatic. We are not, as a rule, conscious of this force, though it may be vaguely felt in the sense of health and the desire for action. But we become vividly conscious of it when it is accelerated by attractions which, in the psyche, promise pleasure, or hindered by repulsions which, in the psyche, mean pain. It is at such moments alone that we become really conscious of having a definite will urging us forward to attain such and such a fancied food, or to overcome such and such an obstacle. The exact significance of this, that we are only conscious of the life-force as our will when it is accelerated or retarded, is not quite clear. But whether affected in this way or that, it is all one force, and it is not free in the sense that it can choose its path. The path will be that which it perceives to be the one of greatest pleasure or greatest safety. This is very obvious in elementary cases; all, at times, admit that only ignorance could have led to such and such actions, and I maintain that all cases

of what we usually call "want of will power," "lack of principle," or "criminal instinct," are in reality cases of defective psychic insight. They are the result of want of experience or insufficient education for the social life, perhaps, though not necessarily, combined with abnormal attractive forces between a particular organic constitution and some special environment. No one persists in eating a fruit which he is convinced is deadly poison, nor would any walk in a path, however attractive it might appear, if he were conscious that it led to some dangerous pitfall which it was impossible to avoid or escape.

But we obtain more light upon this whole subject of free will if we remember what continually brings it to the front. Artificial laws have at different times been promulgated in human social organisms in the hope of obtaining some uniformity of habit, and for the restriction of those too individualistic tendencies which cause internal reactions fatal to the desired social unity. These laws necessarily suffer from all the defects of our psychic perception at the time they were promulgated. Many have been foolish and unjust from the first, and all, even the best, which were perhaps excellent for a time, are outgrown, and have thus become harmful restrictions on liberty.¹ In addition to useful laws, moral laws relating to superstitions have been issued by the churches. Against these artificial social and religious restrictions the life-force cannot fail to drive us, our wills being thus

¹ "Es erben sich Gesetz' und Rechte
Wie eine ewige Krankheit fort;
Sie schleppen von Geschlecht sich zum Geschlechte,
Und rücken sacht von Ort zu Ort.
Vernunft wird Unsinn, Wohlthat Plage."

GOETHE.

inevitably brought into prominence. We obey or not according to our psychic perception. If the attractions of the natural environment are very great, and there is no adequate belief in the bogies which are set up to drive us into obedience, then we go the way of the attractions and are called self-willed and sinners. If, on the other hand, we have been duly trained to see the advantages of the law and the reality of the dangers threatening its neglect, then we go the way of obedience, for we perceive it to be the best. No freedom of choice is needed, we go automatically according as the pros or cons turn the scale. This process, however, looks like free choice to the outsider who cannot see the inner mental processes of weighing up these pros and cons as the individual perceives and estimates them.

There is, however, one very strong subjective argument, which supports the assumption of free choice. Our self-consciousness seems to tell us with no uncertain sound that we are individually responsible for our deeds. This feeling, however, has a very simple explanation as a reflection on our psyches of the mental attitudes of those around us, who always seek to cast the blame of what they do not approve on the shoulders of those most associated with, or mixed up in the offence. But, of course, if there is any truth in our description of the psyche as mainly a perceiving organ which, like all other sensory organs, is liable to error, neither the blame of others, nor the feeling of personal responsibility need be any reflection of the actual truth. Blame is due to superficial judgment, and yet this blaming mental attitude of his fellows is enough to account for the feeling of guilt in the mind of the so-called criminal. Our "knowledge" always

begins with superficiality, and is corrected as we advance to a profounder insight into the environment. When we say "we choose" or "he chooses" this or that course, we express a superficial perception of the action; we cannot perceive either the tangle of forces or the complicated perceptions which really caused the deed. The most abject confession is merely the expression of the mind being swept along into harmony with the minds of those around, like the cringing of a dog on being scolded, even when unconscious of his offence.

That this is the true explanation of that self-blame which is thought to be such a strong argument in favor of free will may be gathered from the fact that "sin" sits easily enough on the mind until it is found out, or until there is some apprehension of its being found out, while it speedily disappears if, when known, it is excused or forgiven. Given "just" laws¹ and proper training in them from childhood upwards, there would be little or no crime among sane people. What remained would be due to madness, *i. e.*, to the abnormal distortion of psychic perceptions.

There is thus no place, I repeat, for any freedom of will, in the ordinary sense of the term, in our rhythmic scheme of evolution. In a certain ideal sense only has the life-force the freedom, say, of exploding gunpowder. An explosion seems free, inasmuch as it overrides obstacles that are not strong enough to resist it, but it is conditioned by those that are, and it goes along the path of least resistance. The life-

¹ "Just" in accordance with the highest perception as to human relationships prevalent at the time. Unhappily, the legal idea of justice is invariably far behind that of our psychic perceptions and not seldom in glaring contrast to them.

force does the same. It drives along the path in which life is possible; here and there, when it has the power, it may be cannibalistic, because that seems the path. The fact that human life, having psychic perceptions, is no longer conditioned by physical attractions and repulsions cannot help the advocate of free will, because it is now still further conditioned by these psychical perceptions.

The view of the psyche in Man as an organ of perception, advocated in this chapter, and of psychic evolution as the gradual development of this organ, is in complete harmony with what appears, in former periods, to have been the chief purpose of organic evolution as a whole: the exploration of the cosmos. Organic life seems to be storming through the universe like a ferment, forever breaking down larger areas of the medium, but then, unlike a ferment, assimilating them psychically as knowledge. Few facts are so astounding to contemplate as that Man, as a social unit, with a psyche growing by constant contact with other units, finds himself, though risen from the mud of some small puddle on the surface of this earth, calculating the orbits of celestial bodies, discussing their sizes, their weights, and their chemical constitutions. In all these mysterious excursions of the mind, above and beyond this earth, on whose face he is but a speck, Man is climbing, by perception after perception, as if up a ladder built, rung after rung, out of the physical facts found existing in his own immediate three-dimensional environment. And, simultaneously, in his religious and his psychic dreams, he is instinctively and inevitably throwing out into space other ladders, built up as accurately as he can out of such psychic

elements as he finds existing in his social environment. As reflections of absolute truth, his results are necessarily premature, for the ideal of human relationship has still to be evolved, but he is advancing. God, the arbitrary tyrant, whose ferocity has to be appeased by gifts, gives place slowly to the more ideal relationship of a father to his children or to the calm superiority to all earthly troubles of a mature and benevolent wisdom. To what highest truth Man will ultimately attain we cannot as yet even guess.

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CHAPTER XXVI

THE FIFTH EVOLUTIONARY PERIOD—THE INTEGRATION OF THE HUMAN AGGREGATE

WE have now to return to the consideration of the fifth evolutionary period, tracing, so far as we can, the progress made, up to the present time, in the integration of the human aggregate in the light of our discussion of psychic phenomena.

The human aggregate must necessarily differ greatly from the aggregates of former periods, because the "Mind" has appeared and has developed in Man; a new factor, and one which may modify the whole process of integration, has consequently to be taken into account.

Such claims have been made for the mind of Man that some hesitation in approaching our subject is natural. Man has been viewed as a being apart, *i.e.*, without reference to an environment. Man and his mind have, indeed, towered up before our imaginations, the environment being regarded simply as the level plain upon which Man stands erect, his mind mingling aloft in the heavenly mysteries. But this conception has to be replaced by a new and, I think, a more inspiring one. The vast height is the environment up which Man is laboriously climbing; he is endowed with sensory organs to aid him, organs which become more and more complex according to his need.

His mind is now but the sum of all his powers of perception into the physical and psychical elements which form his environment. This view enables us to look at all the factors of life in a new perspective; we see Man in his place in the evolutionary scheme and we can analyse the purpose and drift of some of the most puzzling problems of life¹ in a way impossible before.

The special difficulties that meet us at the very outset of any attempt to discuss the fifth evolutionary period were pointed out in Chapter XXII. The unit Man, we saw, is a far more highly developed and complicated organism, both physically and psychically, than the unit of any former period. Equipped with a highly developed nervous system and new psychic powers, he has to become adapted to an increasingly complicated physical and psychical environment before he can combine to build up successfully the social aggregate, a process which is rendered still more difficult by the fact that human units are physically free from one another, being united merely by psychic bonds. It is of special importance that we should bear in mind this morphological freedom of the unit Man, for it helps to explain the confusion that has hitherto prevailed in all attempts to build up satisfactory social aggregates.

We may assume that the first groupings of the human units, arising from the instinctive clings of individuals bound to one another by ties of parentage and of sex attraction, began while primitive men and women

¹ *E.g.*, that of his moral perceptions. These are his duties to his environment, the environment of each unit being the complex of other units among which he is, so to speak, embedded.

were still arboreal, and it may have been these groupings which led to their descent from trees in order to huddle together in caves or sheltered places. But however this may be, it is when the young or, as it may be called in this connection, the "larval" society emerged from the forests to wander in the open as a new organism that the changes it underwent can be visualised with some certainty.

It must be remembered that the early community had to roam about over a hostile country, fighting against foes and obtaining food under great difficulties; any stragglers from the main body would run the risk of being cut off by wild beasts or by rival societies which might prove still more dangerous enemies. The safety of the community lay in vigor of defence or rapidity of flight. In order to survive and to obtain what it needed, the human organism at this stage had to work like an automaton. Its free, predatory life closely resembled that of a beast of prey, and the corporate body had to become differentiated almost like the body of such an animal. The psychical bonds between the component units, the ties of sex and parentage, and the gradual discovery that union and co-operation were advantageous might, under favorable circumstances, be enough to hold a community together, but, when moving about in a difficult environment, surrounded by foes, it had to become differentiated if it was to escape annihilation. As in a predatory animal, there must be a directing brain, a leader of swift perception, of great daring and able to command obedience; seizing and fighting organs were also essential, a military caste, to act as weapons of offence and defence, assisted by scouts as the ears and eyes of the body; while, in the most sheltered

position in the moving mass, protected as much as possible, were the women and children, the former functioning as the reproductive gland of the organism, and also attending to the feeding and many minor duties of the community.

That this was the characteristic organisation of the earliest societies is known, because some societies still exist in this primitive condition, and others, that are gradually changing, show traces of the original order.

Actual morphological differentiation of human units was, however, impossible, for such units were no longer the plastic organisms of the past. Consequently the differentiation absolutely indispensable to the existence of the early communities in which the first head-man work of co-ordination and organisation had to be done could be nothing more than a temporary expedient.¹

The "larval" stage of human society, with its rigid organisation, after bringing Man through the earliest trials, resulted in tribes too big and unwieldy to wander any more. Being strong enough to resist the ordinary dangers, they settled down in the more habitable environments. Between these early settled communities there were still frequent struggles but, in time, amalgamations took place, the fusions being in some cases compulsory, in others resulting from agreement.

Now, a change from a free-living to a sessile manner

¹ The only units that were at all successfully differentiated were the women. The effect of the subordination of the women of all classes from those early times until comparatively recently, of their restriction to the sex interests of the race, under regulations made by man, as well as of the uniform and monotonous life to which they have been doomed, are still felt.

of life necessarily involves a number of morphological changes in the human as in any other organism. Sessile organisms tend to lose the special characters essential to free life, such as locomotion and the capture of prey. The organisation becomes diffuse, sensation is no longer concentrated at one point, but becomes equalised all over; the guiding centre becomes disorganised, and the whole organism spreads out, as it were, and roots itself to the ground.

Although the physiological needs of a stationary society must, in many ways, differ from those of a wandering tribe, the fundamental problems of its existence remain the same. The food supply and its proper circulation among the members of the community are still of the first importance if the organism is to remain strong and healthy. In human societies this entails the wisest and best application of industry and intelligence to the cultivation of the soil, the prevention of waste, the ridding of the organism of parasites, etc. Another fundamental necessity is that of healthy reproduction, and of the bringing up of the young and, so that the life functions may be pursued in safety, the organism must be prepared to defend itself or even to attack other organisms if that is the best policy of safety. These are, indeed, still the fundamental problems of the amalgamated societies of to-day, except that, as amalgamation extends, the need for warlike operations should claim less of human activity.

When nomadic life ceased and the conditions of life changed, there was no longer the same need for that subordination of the majority of the community to the minority which was inevitable under the stress of those early days, but which is fundamentally un-

natural and repugnant to the free human unit. This fact, however, has not been realised, and it is, I believe, this long-continued attempt to achieve the impossible,—to subordinate morphologically free and equal units, that is at the root of the misery of mankind throughout the ages. It is this which seems to supply the key to the confusion still reigning in the social organism.

The early historical records which tell us of the struggles between the early nations and races, show them all simultaneously torn by internal factions, the disputes invariably turning upon the impossibility of satisfactorily differentiating the units of the community. With endless and sickening reiteration, leading families win, strive to retain, and eventually lose the leadership granted in time of danger, the military caste taking sides with one party or the other. When the leadership factions are strong enough, they invariably divide the wealth of the community between them, dooming the majority of the people to poverty and monotonous toil. Hence, ever and anon, when in their turn strong enough, the workers rise in rebellion against their evil plight and add to the confusion. Meantime, the females of the community remain in subjection to the males.

The significance of all this is only fully perceived when we realise that the inner evolutionary forces were forever prompting each individual unit to claim equality with the rest, and to demand equal rights and freedom, promptings which were invariably counteracted by those in power by doctrines of submission, the struggle being made more terrible by the dread of some great supernatural power behind the human authority, which took on terrible forms in the human

imagination,—forms appealed to and against as if they also were actual living forces capable of miraculous intervention in human affairs, and of wreaking vengeance the very thought of which struck terror into the breasts of the boldest of men.

And now, coming to modern times, we find vast amalgamations of the earlier communities, great nations, peopling all the immediately habitable parts of the earth, and gradually learning to live side by side without continual conflict. Their common interests are increasing and are being more recognised; they are becoming bound together by ties not only material but sympathetic. And yet, in spite of the important changes undergone by the human organism since the time when it resembled a wild animal, the distinctions which were necessary to its existence only at that stage of its integration still persist. This is chiefly owing, no doubt, to the useful subsidiary functions served by them. Like vestigial organs, however, they must in time disappear. The predominance of the families of the leaders and the supremacy of the military caste, having served their temporary purpose, are doomed, sooner or later, to vanish. We actually find, indeed, that all the forces of the dominant classes, with all the civil, military, and ecclesiastical¹ power at their disposal, are less and less able to counteract the instinctive demands of the great mass of the human units for equality; the residue, so long down-trodden, have already, inch by inch, won some measure of recognition as equal units of the human aggregate.

¹ It is evident that the specious appeals, made in the past, to the "spirits" of the environment (spirits that have even been represented as similarly differentiated in their own world) in order to try to give stability to arrangements that were rightly only temporary expedients, are losing their force.

This marvellous persistence of equality among human units in spite of the age-long attempts to differentiate them is, indeed, one of the most instructive facts in the biological history of man. The thousands of generations during which the leadership system endeavored by every possible and impossible means to differentiate the race into royal, aristocratic, and slave classes have had no appreciable effect. A prince may at any moment give birth to a slave, and a slave to a prince. The young units appear and grow and are, as adults, simply what the social organism allows them to become. The purely artificial social rank of their birth is a factor of no account, for they respond automatically to the environment in which they are brought up. Reared in the soft luxury of a palace, they tend to become effete; brought face to face with the natural environment, at the plough, on the sea, or in the forest, they develop the more virile characteristics. This irrepressible claim to unit-equality on the one hand, and the fact that the poorer classes have furnished no small proportion of the great minds of the world on the other, may be claimed as witnesses from the field of biology to the essential truth of our morphological argument.

It is thus evident that, in spite of the amalgamation of nations tending to peace, and in spite of all the boasted "civilisation" of modern times, the fundamental problems of social life are still far from being satisfactorily solved, *i.e.*, the social aggregate has not yet attained a condition of stable equilibrium with regard to its external material and its internal psychical environment. Any real advance in this direction seems impossible until harmony is established between the component units of the organism. If so, the grad-

ual removal of the artificially continued distinctions between these units is essential.

The true direction of the evolutionary path has, I believe, been obscured in several ways, which we must now briefly consider.

I would point, in the first place, to the economic confusion which resulted when, for lack of environmental stimulus, the attempts at morphological differentiation began to fail. The dominant classes, in the early settled communities, had divided the wealth of the community between them, and the masses lived as dependents under their protection. This was the economic basis of all the leading nations in the middle ages, a system which, however, had to give way before modern conditions. The so-called "free" individuals who now compose the mass of the population have to live as best they can, and the natural desire to possess enough wealth to live and to live fully, on the one hand, and the dread of poverty on the other, have brought about a merciless scramble for wealth, and even for mere existence. It seems almost as if an insane delirium had possession of human societies to-day, blinding them to the cruelty and folly of this deviation from the real path of evolution. The Black Hole of Calcutta was an isolated freak of one oriental savage, yet the recital of it fills the world with horror. But that same world is now rushing on blindly, manufacturing slums in almost every city and town in the world, slums in which the crushing out of human life, and hopes, and possibilities is more protracted, more destructive and far-reaching in its baneful influence than was that one outbreak of oriental ferocity. So terrible is this universal modern cruelty, that it is only explicable as a blind rush, resembling

a panic in a herd of cattle. Even the naturally unselfish and kind-hearted are swept along by it, regretfully admitting that they have no time to listen effectively to the cries of distress of those who are trampled underfoot. A mad individualistic rush, each one for the security and, as far as possible, beautifying of his own personal environment, turns civilisation into a pandemonium and human life into a hell of feverish desires which, as the dice fall, may be answered either by a surfeit of good things which leave the soul empty and dissatisfied, or more frequently by misery and starvation. The highest manhood is destroyed alike by failure or success in this struggle, and the true path of evolution is temporarily obscured.

Another cause of the true view of evolution being obscured is to be found in the trend of latter-day philosophic doctrines. The organic unity of society, almost axiomatic during the eighteenth century, received great checks in the nineteenth, from the spread of doctrines which either actually conflicted with it or were thought to do so.

The philosophic attempt to systematise the principles of material wealth, made by Adam Smith, was, in itself, a magnificent assertion of liberty as against all the artificial restrictions with which the dominant classes had sought to hamper trade in their own interests, but the solidarity of the race was not part of Adam Smith's theme. He dealt with the principles of exchange between man and man in a purely mechanical way, uncoloured and unqualified by any of the vaguer and more spasmodic human sentiments such as generosity. It would have been impossible to systematise a subject if all its deductions could at any moment be completely upset by some chance explosion of

sentiment. Hence the principles of business were founded upon the assumption that men were not, in any essential way, bound together, but were mere individuals, each driven by his own immediate wants. This was mere matter-of-fact observation. It did not pretend to be a statement of the whole law of human relationship, but was offered as a reasonable basis to argue from and as true for practical business purposes. Indeed, it has to be accepted and will have to be accepted as a basis for all practical working of society through all time. Let the human relationships be what they may, there will still be vast fields of social work in which each unit will practically be but a cog of a wheel, at best an intelligent and willing cog, for only so will the machine work. Any protest he wishes to make, so as to be able to express himself more thoroughly, must be made when opportunity offers, not while the machine is working.

Quite mistakenly, this great work on political economy seems to have had the practical effect of endorsing a doctrine of hard individualism, and of obscuring that of solidarity.

Then came the development of the doctrine of evolution, set out as chiefly the result of struggle and the survival of those who could triumph over the rest. It was plausible, partially true, and easy to understand, because it fell in well with the wave of individualism on which our industrial system was running its ruthless course. A successful minority was reducing the poorer and helpless masses to the position of wage slaves, to be used as long as their physical strength had any market value as labour, and then to be thrown on the rubbish heap. This gave the Darwinian doctrine of natural selection an accept-

ance out of all proportion to its real philosophic value. The greatest objection to it was naturally not easily seen, because the part played by colony-formation in the evolution of life had not then been emphasised. Had the gradual development of social life been recognised as the integration of a colony, a doctrine of life-and-death struggle between the component units would have appeared an absolute impossibility, for the perfecting of a colony into a compact organism can only be brought about by co-operation and mutuality. One of the greatest thinkers of the time, Herbert Spencer, declared quite plainly that natural selection alone did not satisfy him; he preferred the earlier and truer doctrine of evolution as expounded by Lamarck, the doctrine of the gradual and direct adaptation of an organism to the environment, which our evolutionary rhythm tends to endorse. But Spencer also had no clear vision of the organic unity of human society. To him it meant nothing more than a congeries of individuals, joined together mechanically and mutually dependent upon each other's efforts, kept in order by a set of moral doctrines, upon the improvement of which the advance of society, he thought, depended.

One of the most dramatic figures in relation to this philosophic controversy was Huxley, upon whom the burden of the life-and-death struggle weighed heavily, as it must upon all serious thinkers. Not long after this gloomy view had received a great accession of strength from Weissmann's germ-cell theory,¹ which

¹ Weissmann's observations on germ-plasm will doubtless find a place in the morphological work of the future, when the true morphological value of the cell is perceived, but the bearing they were supposed to have upon the doctrine of evolution was vitiated by the assumption that the cells of the embryo are as separate and distinct from one another as billiard balls piled together (see above, p. 94).

gave what appeared to be the *coup de grace* to the teachings of Lamarck, leaving natural selection in sole possession of the field, Huxley delivered his Romanes lecture on "Evolution and Ethics." In eloquent language he set forth his view of the terrible drama of life through which mankind had to pass. He described human society as composed of so many wild beasts struggling fiercely and mercilessly, each against all. From this conflict there could be no shrinking, no escape; he had no consolation to give his hearers: "Quit ye like men" was his only exhortation. Ethics, for the moment, appeared to him as some new life-process coming in as a slight mitigation of the terrible cosmic process. Not until the lecture was in print did a footnote appear to the effect that colony-formation and social life were also, of course, products of natural evolution and thus also parts of the cosmic process. This, indeed, was the truth to which Huxley's generation had been temporarily blinded.

When these obstructing philosophical views are assigned their true value, there is no reason why Man should not wake up finally to a truer conception of human society as an organic whole, and of himself as essentially the unit of the social organism. As such, he cannot attain to full and healthy life through a life-and-death struggle with his fellow-units. By such a struggle he can gain only the intense excitements of the gambler, the moments of suspense, the suppressed bitterness of defeat, and the cruel triumphs of success, sentiments, surely, with which no life above that of the proverbial serpent can be filled.

The goal of evolution in its action on organic life at its present level of development is, as in all previous periods, the production of organic units adapted for

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efficient and harmonious responses to both internal and external stimuli. The process has hitherto been a blind one; the politics of the present,¹ and the history of the past, may be regarded as blind and unsuccessful attempts to produce such units. So unsuccessful have these attempts been that we are still surrounded by the clashing of rival interests in the midst of which the individual feels himself helpless, like one tied to the wheel of a great machine, the purpose of which he altogether fails to understand. We are the units of a colony in the throes of integration. The subordination of individual desires and impulses in the interest of the aggregate, painful enough in colonies of earlier and simpler units, is now still more painful. There is now no direct nerve stimulus sweeping through all the units and carrying them along with it. A multitude of stimuli from all directions wake up our dominant desires and impulses, and we act as seems most desirable to ourselves, but in complete darkness as to the result of our actions. Laws and moral precepts have gradually been evolved for our guidance, but they have never been very efficient. The laws have generally been behind the date, while the moral precepts have been too ideal and impracticable for the life that had to be lived. Man has thus failed, in every age, to obtain efficient guidance, which can satisfy his deeper instincts, as to the nature of his intercourse with his fellow-units. Let us take, by way of illustration, the practical moral codes of to-day. They have been cast on an individualistic basis, that is to say, they are only suited to an earlier stage in the integration

¹ All politics are, in reality, morphological phenomena, though we do not see this because of the dust raised by the wrangling interests of the present.

of the human aggregate, when human societies were regarded merely as congeries of separate individuals who fulfilled their whole duty by living and letting live. Expressions of human sympathy and help were considered graces, not duties. The law was concerned only with the rights of individuals. But it has now long been perceived that this is not only not enough but so inadequate for modern requirements as to amount to positive immorality, and some new code is demanded. It has so far been impossible to formulate one for want of clear vision as to its basis. This want our evolutionary theory supplies, by showing that we are not a congeries of separate individuals, but the functional components of a new social organism. It is no longer possible to "live and let live." As units of one organism, we share a common environment, and our lives, physically and psychically, are intimately associated with the lives of our fellow-units. If, at any moment, we draw with special greed upon the physical environment, we are robbing others. We are doing the same if we keep our psychic perceptions, our feelings of humanity and sympathy, to ourselves. Our primitive unit-morality has done its work; it is now behind the age, for social integration has advanced. "Thou shalt not murder, nor rob, nor be violent, nor do injury of any kind to thy neighbor" is no longer enough. The command should now run (if we must keep our laws almost purely negative, which appears to be the wiser course): "Thou shalt do nothing, directly or indirectly, nor acquiesce in anything which injures the common environment, either physical or psychical."

Poets and seers, in all ages, have dimly foreseen that some such change had to come over the life of

Man, and by their visions have awakened and fed his hopes. The founder of Christianity, with marvellous insight, realised that the social psyche was one, and one with the universal psyche. The most perfect psychic harmony was his ideal, to be attained by every human being living out the doctrine of universal love. Small fragments of his doctrine have become current coin, but there is as yet no vital perception among the mass of men that society is not a congeries of individuals, but an organic whole, and that there must be an end forever to a fierce "struggle for life" among its units.¹

The time for blindness is now past. The developed psyche of Man has to come to the aid of evolution; the human aggregate has to become, deliberately and consciously, what it is morphologically, an organic whole, the units that build it up recognising the end to be attained, and endeavoring to organise life with that end in view. The blind eagerness of each unit for the betterment of his own environment, which results in the shrivelling up of the individual psyche, poisoned by the misery of its fellow-creatures, has to be replaced by the desire for the cultivation of the whole human environment. The very way in which

¹ The difficulty in realising this lies chiefly in the relation of the ordinary individual to the physical environment; on account of undeveloped psychical perceptions, the doctrine sounded and still sounds unreal to the majority. While the psychical element of the environment might admittedly be one and indivisible, it is not so easy to see that the physical environment is also a continuum. Consequently we find that still, 2000 years after psychic unity was proclaimed by the greatest genius of the Jewish race, Man is prevented from consciously and deliberately living in harmony with his fellows because of the impossibility of arranging for any fair division of the physical environment, or of "property," the name given to those endless subdivisions of that part of the physical environment that can be monopolised by individuals.

mankind has been swept along the paths now seen to be wrong shows clearly the true line of advance; the gradually vanishing traditional or hereditary impulses have to be overmastered by a spirit of co-operation and mutual dependence, and the merciless element of competition has to pass into and be replaced by a friendly rivalry in the service of the common cause, or in the attainment of some excellence desirable for the whole organism.

The first step in the right direction is to secure the equitable satisfaction of the physical and psychical needs of each individual so far as our mastery of the environment of the moment permits. A perfect circulation of all that is necessary to the fullest human life, physically and psychically, has to be established. None must be allowed to suffer either from the physical impoverishment resulting from shortness of the necessities of life, and the overstrain of dull and monotonous toil, or from physical deterioration caused by idleness and luxury. And, since man does not live "by bread alone," the demands of the psyche in him, such as the thirst for knowledge, the craving for liberty, justice, human sympathy, must also be satisfied. These are only some of the psychic claims now to be taken into account; as these are fed, it is likely that others will unfold in endless variety, others possibly as far out of the range of our present power of comprehension as modern science is beyond the range of an Australian aboriginal.

The work by which the world's wealth is produced will go on, but the wealth that results must be spent, with the full and hearty agreement of those who now blindly monopolise it, on experiments as to the best way of giving every human being an environment

which will bring out his noblest qualities as a man among his fellow-men. The full measure of the mental stature of man has never yet been reached, even by the greatest genius the world has produced. Indeed, may not the genius that now springs up sporadically from scattered parts of the human field be a prophecy of the general level of intelligence in a more harmoniously co-ordinated social aggregate? Each unit of the aggregate possesses the possibilities that lurk in the human psyche of catching, as it were, and reflecting for its fellow-units, in some beautiful way, the rays of the cosmic psyche. It is obviously the wisdom of Man to till the whole human field carefully, attending to the cultivation of every unit, and developing to the full the individual capacities that are of inestimable value to the whole race.¹ May we not expect that, as the human unit becomes perfected, it will attain to new and hitherto undreamt of manifestations of psychic force, and that social life, deliberately worked

¹ Of every unit, regardless of sex. From women, as free and equal units, much may be expected. Differing as they always must, in certain respects, from men, they may prove to have special psychic perceptions of which men may be constitutionally incapable. A specially rich harvest may also be expected from the great ecstasy of human love when disentangled from the present economic conditions and no longer a thing to be bought and sold or made the subject of a legal contract.

Only by such free development of all the units can a human society escape the fate which organisms of past periods brought upon themselves through the stiffness of their skeletons and the consequent withdrawal of large numbers of the units from sensitive contact with the environment. The rigidity of human institutions which blind and cripple vast numbers of units in the supposed interest of the whole society, may well be compared to the rigidity of the coral skeleton which drives whole colonies to acts of suicide (p. 295 and Fig. 45). The result must be the same in both cases. A human community that does not free itself from its artificial limitations in the interest of unit freedom and unit cultivation must, like the corals, drift to one side of the evolutionary stream.

out according to the highest wisdom of mankind, will rise to a new and higher physical and psychic level?

And does not the fullest life of the individual unit involve, essentially, harmonious relations with his fellow-men? There is a story, told by Lecky, of a leading Indian official who, on being congratulated on the pleasure he must feel at having brought to its conclusion a problem which had tasked all his energies for many years, replied: "As for the pleasure I feel, it is nothing to what goes through me when I hear the feet of that child pattering along the corridor!" It is such simple things as these—our loves, our friendships, the eager exchange of views and sentiments with companions, every one differing from the other, this one humorous, another serious, another always fascinating because of the strange elevation of his thoughts, another, again, equally so because of his whimsicality—it is these that constitute the true, full life of the human unit. These are the threads that weave the richest life for Man. Outside of this ordinary intercourse, there is that which is less close and personal. We all listen in spellbound attention to one who has the gift of oratory or of story-telling, to another who expresses deep emotions in exquisite sound, or to those who charm us with their skill in rendering the musical creations of rare genius. We gather in crowds to see the works of great painters. We listen with eagerness to the messages brought to us by those who are searching into the mysteries of the cosmos which science is little by little unravelling. These are the things which contribute to the full life of human beings, and all without exception are variations of one and the same thing: intercourse with our fellow-creatures. Intercourse with Nature and with God plays its part

also in human life, but cannot altogether satisfy, for, like travellers standing on the shore of some vast ocean, the indescribable majesty of which merely overawes them, we feel driven back to the haunts of men, though, strange to say, driven back the less imperatively the more deeply our human sympathies are cultivated.

These facts are fully endorsed by our evolutionary principles. It is now as it ever was. Organic life means adjustment to the environment. Life is full or meagre only in association with that environment. Contact experiences form the coherent sequences which together make up the individual life story. Those have the richest and fullest lives who have the greatest number of environmental contacts, and the most enjoyable. It is the fact that our fellow-units thus wall us round and constitute the real medium in which we live which renders artificial distinctions of wealth, rank, education, and training impoverishing, for they tend to cut us off from much of that human environment from which emanate our joys and our sorrows, indeed, all our sentiments and emotions, from the lightest of rippling laughter to the profoundest of mental agonies.

I am aware that these are commonplaces, but life progresses through the recognition of the real significance of commonplaces. Nothing "comes from the blue"; Man only slowly learns how to interpret his environment long after it has enveloped him. The scenes shift as we stand or move about on the stage, and we wake up very gradually to see that the play has to change.

We can thus, to some extent, foresee the line along which the human unit must develop in order to become

efficient for the purpose of building up a harmonious social organism, and we may conclude that the further development of the psyche, so far as the unit is concerned, will proceed naturally with the deepening of human sympathies and the increasing intimacy of units all engaged in the service of the community.

The details of the further integration of the social organism are, of course, hidden from us, the units of to-day, but I would venture, before closing, on a few general considerations and suggestions with regard to this process.¹

In the first place, we have to recognise that the human colony must, in the method of its integration, differ from the colonies built up in former periods. Consisting as it does of separate units, it is obviously impossible that it should become centralised in the same way as the aggregates of those periods, in order to produce a new organic whole. Human aggregates, so far as we can see, must, for all time, be human aggregates, *i.e.*, groups of men, women, and children. It appears impossible that such aggregates can assume any new physical form. The brains of the human units cannot be thought of as fusing into any corporate

¹ It is quite impossible here to enter on the vast question of the integration of all the various branches of the human race into the complete human aggregate. We can only assume that evolution will gradually bring this about. We may surely expect that, the more self-conscious and intelligent the nations become as organisms, the more will they agree to settle their disputes by reason and arbitration, realising their true evolutionary destiny, the lifting up of the human psyche into regions which promise to surpass, in pleasurable excitement, the wildest dreams of ancient mystics yearning for paradise. Armies for the destruction of their fellow-men will give place to international police while the nations equip themselves for the storming of the psychical environment.

centralised brain for the whole social organism. At the most, we might compare the social organism of the future to one vast brain spread like a film over the surface of the globe, composed of units, highly organised individually and in their interrelationships, but without form in the aggregate.

At this stage of evolutionary progress, consequently, there appears to be an abandonment of the method of advance which, in earlier periods, seemed essential, but I think that some light is thrown upon this apparent anomaly if we consider why the successive changes of form of earlier periods were necessary. The unit of each former period was, as we saw, that organism which was most sensitive to environmental contact and, at the same time, most perfectly centralised for the co-ordination of the environmental stimuli which it wove into coherent sequences of sensations, thereby gradually developing knowledge of the environment. The object of the morphological transformation seems, in each case, to have been the perfection of a nervous system as the organ of the psyche for more efficient advance in physical and psychical adjustment to the physical and psychical elements of the environment. Each organism was a physical machine necessary to keep this nervous system efficient and to carry it about in order that it might come into contact with the widest range of the environment possible for its special level of complexity.

In this fifth period, the nervous system of the unit has been developed to such an extent as to be almost commensurate with the physical machine. The purely physical life of Man has contracted to very small proportions as compared with the physical life of previous units. Great physical activity is no longer

essential; it is the psychic energies that have chiefly to be efficient. The life-force no longer seems to be driving the organism hither and thither through the physical environment, but rather to be concentrating more and more on psychical development. Indeed, the physical environment, knowledge of which has to be obtained by physical energy, may be said to be practically exhausted. There are still a few regions of the earth to subdue and occupy, but no one doubts that Man can and will do this work when it requires to be done; there are still insidious foes to be warded off, mostly in the form of invisible germs which run riot in the tissues of the human body, but these are probably the last of Man's organic foes, and he is gradually learning how to defeat them. The physical environment still holds within it subtle secrets of its mechanism which must continue to exercise the brain of Man. But with these exceptions it may be considered to be practically mastered, Man's psychical faculties having been highly trained in the process.

The fact that human societies owe their very existence to primitive psychic bonds, combined with the marvellous development of the psychic powers of Man, seen not only in their ever-wider application to material things and mechanical devices, but in the diffusion of knowledge and the spread of new ideas, seems to indicate that it is the psychical element in Man that is destined to become more and more specialised. The psychic element of the environment also which, in this fifth period, has burst, as it were, upon human view, perception of it being quickened by social life, seems to be the element of the environment to which Man has specially to become adapted and which he is just beginning to explore. We are driven, as we

saw in a former chapter, to postulate the existence of a cosmic psychical environment co-extensive with the physical cosmos, but we can only speak of it as something into which organic life has gradually been growing and which, for the future, is likely to be the great environmental factor. Psychical phenomena, as we can at present appreciate them, are too various and mostly too subtle and transitory to admit of any but the crudest attempts at co-ordination. Experimentation cannot possibly be exact, because of the multiplicity and extreme subtlety of the factors.

We may compare our ignorance in this respect with that of one of the units of the fourth period as to the nature of a garden of flowers. A whole evolutionary period had to be passed through before an organism was produced capable of the most distant comprehension of the beauty and variety and purpose of so simple a complex. So it is with Man. He is not yet high enough in the evolutionary scale to appreciate the true significance of a psychic environment. He is now endeavoring to co-ordinate phenomena with the view of arriving at some intelligible theory as to the real nature of electricity; with psychic phenomena he has not yet reached even that stage of investigation.

The physical universe, already to a great extent rushed through by organic life, may thus, I think, be regarded as the lower dimension of our environment, evolution having now brought us into a higher psychical dimension as the real objective of life. If so, it would appear that the life of the future will be the result of the interplay of the specially developed psychic organism with a psychic environment. May we not see, in these changes, some reason for the abandonment of any further morphological transformations?

Returning, for a moment, to the uniform distribution of the perceiving organs of the units throughout the human aggregate, I would compare these to an infinite number of lenses focusing, with different degrees of definition, the physical and psychical rays received from different areas and depths of the environment, and I would suggest that these different perceptions may be thought of as running together within the organism into higher and more complex perceptions, the social psyche being thus developed. May we not see, in some such building up of coherent sequences of new psychic perceptions, the approach of a condition of perfected social sensitiveness analogous to the condition characteristic of every former unit? May not this be the process of the future by which the unit of the sixth evolutionary period will be produced,—a unit perfectly equipped for storming and exploring the cosmic psychic environment? What such exploration would mean, however, cannot be expressed in terms of life as we know it to-day.

The difficulty in conceiving any future evolutionary stage is no argument that there is none still to come. Who could have foretold the cell, knowing only the chromidial unit, or, indeed, how could any of the units or of the periods have been foreseen? We are justified, I believe, in assuming that the evolutionary series I have sketched will continue and that the evolutionary path will carry life onward to still greater heights. Any pessimism about the future finds instant reproof when we look back on the past.

Our organic rhythm has now been traced, sharp and clear, since its rise out of the inorganic to the present time. It fades gradually away as it passes

through the veil of the future in the latter half of period five. Just as it appears to be repeating the law of unit-formation, it vanishes entirely. May we not believe that it rises out of sight in order to start a new period on a higher level of life, one altogether beyond our present comprehension?

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